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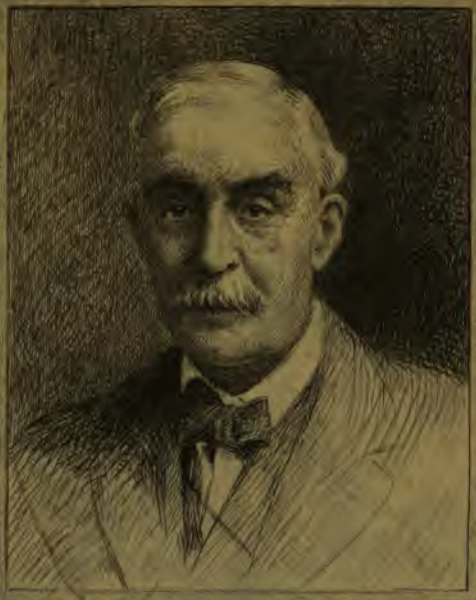

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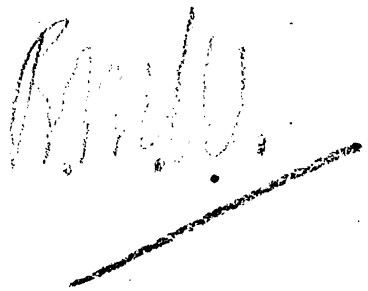

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THE

NATURAL CONDITIONS OF EXISTENCE

AS THEY AFFECT

ANIMAL LIFE

BY

KARL SEMPER

PROFESSOR OF THE UNIVERSITY OF WÜRZBURG

WITH 2 MAPS and 106 WOODCUTS

THIRD EDITION

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PREFACE.

It was Jaeger who once said—but I forget where—that enough had been done in the way of philosophising by Darwinists, and that the task that now lay before us was to apply the test of exact investigation to the hypotheses we had laid down.

C 3-10-39

I have long been of the same opinion; but it is in fact a thing much easier said than done. It is infinitely easy to form a fanciful idea as to how this or that fact may be hypothetically explained, and very little trouble is needed to imagine some process by which hypothetical fundamental causes—equally fanciful—may have led to the result which has been actually observed. But when we try to prove by experiment that this imaginary process of development is indeed the true and inevitable one, much time and laborious research are indispensable, or we find ourselves wrecked on insurmountable difficulties.

Nevertheless the step must be taken. The popular cant about 'Biogenetic principles and the falsification of Ontogenesis—the laws of inheritance at corresponding periods of life, or the correlation of organs—Ontogeny

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and Phylogeny—variability and heredity'—is put out of court as useless, for these are merely axiomatic expressions for a sum of identical or correlative phenomena of which the essential nature is in no way revealed by them. They all still await an intrinsic explanation.

It appears to me that of all the properties of the animal organism, Variability is that which may first and most easily be traced by exact investigation to its efficient causes; and, as it is beyond a doubt the subject around which at the present moment the strife of opinions is most violent, it is that which will be most likely to repay the trouble of closer research.

I have endeavoured to facilitate this task, so far as in me lies, by here presenting a general view of those facts and hypotheses which bear upon the subject and are either of universal significance or, from my point of view, appear to offer favourable subjects for experimental treatment. This list, however, makes no pretension to completeness. If only it should give an impulse to research, on however small a scale, so long as it is systematically conducted and thoroughly carried through—if only it should contribute to extend my own convictions as to the uselessness of casual and disconnected observations, I shall have attained my end.

The immediate occasion of the writing of these papers was a call to deliver a course of twelve lectures at the Lowell Institute at Boston from October to December 1877.

KARL SEMPER.

WÜRZBURG: *Sept.* 1879.

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NATURAL CONDITIONS OF EXISTENCE

AS THEY AFFECT

ANIMAL LIFE.

INTRODUCTION.

No one at the present day disputes the fact that the Darwinian theory has exerted an extensive influence not only on the development of the natural sciences, but in other branches of study; it would be superfluous here to bring forward any proofs of this. It is equally recognised that it is to this influence that modern zoology owes its most essential pretensions to be regarded as of equal estimation with other sciences. But it may be advisable to pause for a moment at the question, In what way is it that this influence has affected zoology? since in this book we have to deal exclusively with this science.

Darwin showed the possibility of discovering the path which nature struck out in order to produce her endless variety of animal forms, and of detecting the means she has employed in her task. Hence first arose those efforts, so natural in the zoologist, to acquire some comprehension of the succession in time of the different types in the animal kingdom, since all who recognise Darwin's teaching must regard it not as an arbitrary and lawless assemblage of independent species, but, on the contrary, as a great family of organisms of which the individual members, whether living or extinct, are united by a real,

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and not merely fanciful, bond of close affinity. The search for the natural genealogy of these families of organisms is one of the grandest of the problems propounded to modern zoology by the great English philosopher.

Naturally enough, in this search, zoologists had recourse to those means and methods which were most familiar to them and which had hitherto been at their disposal. Ever since the time of Cuvier they had been accustomed to discriminate between the different forms of animals and to describe the organs which distinguish and separate them, endeavouring at the same time to detect by them the ideal affinities of animal types. But they were more practised in the use of the scalpel and microscope than in availing themselves of the often highly complicated apparatus and methods of the physiologist, and it is only lately, under the influence of Darwin's views, that they have begun to enquire into the true and natural affinities of animal types by comparing them together as to form, and by studying their mode of origin. Thus it is that the modern study of animal morphology has arisen, commonly divided into comparative anatomy and embryology; but at the same time, equally under the influence of Darwin, zoologists began to devise genealogical trees for the different groups of the animal kingdom—sometimes for a whole group, sometimes for a subdivision only—in which they attempted to give graphic expression to such knowledge as they supposed they had acquired of the actual processes which, through constant modifications of the most widely different forms, led finally to the development of the human body.

Of course such pedigrees could not be otherwise than of a somewhat doubtful character. In all zoological investigations, as in almost everything else, a certain influence may be detected which may be termed the personal element. Zoologists are not, as mathematicians are, able to set out from certain immutable axioms, and to calculate from them the forms and origination of animal types with mathematical exactitude; on the contrary, they are forced to deduce all the laws of their science from observations of phenomena. The mode of carrying on these observations, moreover, and consequently the answer which nature gives to the questions put to her, depend

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essentially on the individuality of the observer. Zoologists have hitherto been equally little able to avail themselves of any aids to experiment analogous to those which are abundantly open to the chemist and the physicist, to the physiologist and even to the botanist. In this respect, indeed, zoologists are very badly off—worse off than any other class of scientific enquirers—for until lately they were simply directed to interpret the facts presented to them by nature, without being in a position to formulate their own problems or to force nature by any critical experiments to give a distinct answer to them. Hence any pedigree selected by one or another naturalist, and based on facts derived from animal morphology, could, and can, only avail to represent those ideas as to the affinities of animals which their author in each case conceives to be the only accurate ones; and hence it must necessarily contain a larger or smaller infusion of subjective fancy and unquestionable error. Thus it is not very surprising to learn that a warm dispute has just broken out as to which group of Invertebrate animals is to be regarded as the closest in affinity to the Vertebrate; nor that the view, hardly of ten years' standing, that the Vertebrata are allied to and derived from the Ascidians, is combated, not without strong reason, by another—namely, that they are more nearly allied to the Annelida—without either side having hitherto proved itself victorious. Subjective views inevitably play an important part in every scientific application of the facts of animal morphology.

We may, however, rest satisfied with these illustrations, and proceed to the wider question, how it was possible that nature should have produced such an immense variety of forms as is exhibited in the animal kingdom, without ever losing the thread of affinity which the zoologist seeks to detect in animal structures and to exhibit in his genealogies or systems. Darwin has here supplied us with the answer. He has shown, as it seems to me in the most satisfactory and exhaustive manner, that two properties inherent in organic beings have contributed, in conjunction with other external natural factors, as means to the accomplishment of this end: First, the power in the parents of transmitting to their descendants their essential

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morphological and physiological characters—or Inheritance. Secondly, the plasticity of the organism, which enables it, by modifications of its original characters, to accommodate itself to the altered conditions of existence in its successive stages of life—or Adaptation.

Hence it directly follows that the problem of the morpho-

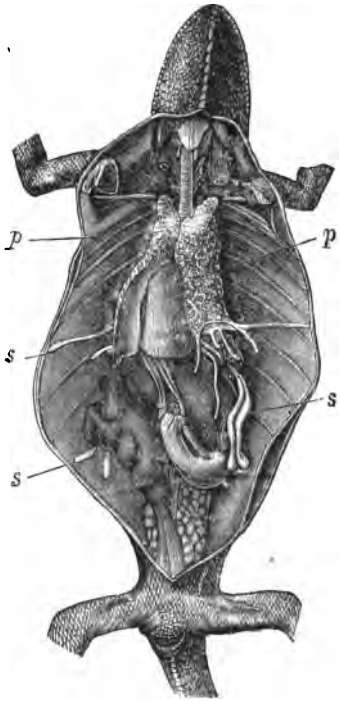

FIG. 1.—Internal structure of a Chameleon in its natural position, to show the lungs, *p*, and the long air-sacs, *s*, proceeding from them.

logist is to learn to distinguish such characters as have been perhaps recently developed by Adaptation, from such as have been transmitted by Inheritance through a long series of generations; for if he should be incapable of making this distinction he will inevitably fall into many gross errors in his attempts to

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establish the affinities or the genealogy of an animal. Since the first appearance of Darwin's well-known work, this has in

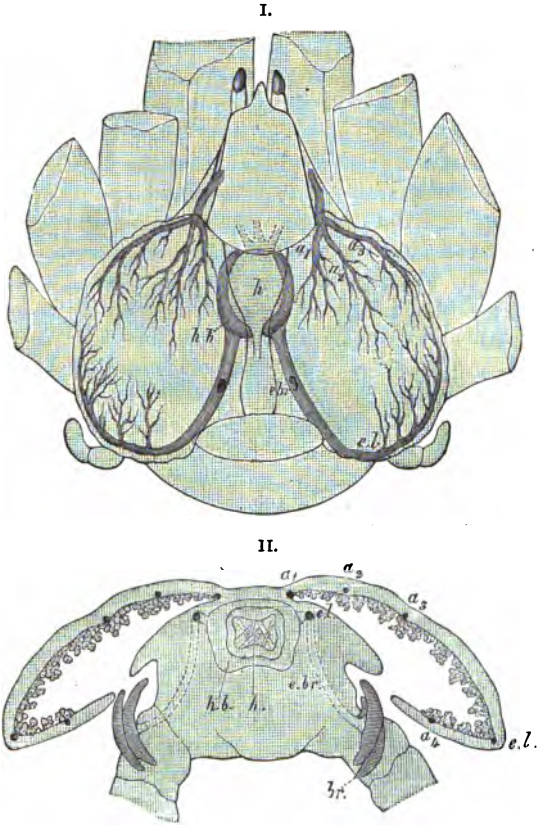

FIG. 2.—Diagram of the lungs and circulation of *Birgus latro*, the Palm Crab. I. The lung-vessels indicated within the outline of the animal—a_1, a_2, a_3, the three upper afferent vessels (veins); *e l*, the efferent vessel (artery); *e b*, section of the opening of the arterial gill-vessel; *h*, heart; *h b*, pericardium. II. Diagram of section of the same, lettered as above—*br*, gills or branchiæ; a_4, the lower afferent vessel (vein); *l*, the lung cavity, showing the pulmonary villi (tufts) on the inner surface of the wall.

fact been the method of modern zoology; and I do not fear contradiction when I say that we have already made considerable advances in the art of discriminating between those typical

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attributes which have been preserved by transmission through long series of apparently very different and yet nearly allied species, and those characters of adaptation which here and there arise, as it would seem arbitrarily, and beyond a doubt quite independently of the affinities of animals. The absolute necessity of clearly separating these two groups of characters will be made plain by the following illustration of one special case in point.

Everyone knows that the lungs of all the higher vertebrate animals are indispensable to their existence; no mammal, bird, or even reptile, could live long without this breathing apparatus. Similarly constructed and indispensable organs for breathing air occur in many Mollusca and in a few Crustaceans. Now, if a zoologist endeavoured to prove that all animals which have organs adapted to respire air must therefore be closely allied, it would hardly be worth while to point out that his attempt must be hopelessly futile. It suffices, with regard to the example I have adduced, to point to the fact that the lungs of the Vertebrata are connected with the intestinal canal and developed from it; while those of Mollusca and Crustaceans (fig. 2) are nothing more than cavities in the side, which have originated from a lateral invagination of the outer skin. But an organ which, like the lungs of mammals and birds, takes its rise from the intestinal canal, can never have originated in a modification of the outer skin, or epidermis. This proves that the lungs of different groups of animals must have originated independently of each other, and that we are justified in regarding them as, in some degree, characters of adaptation.

Another instance. It is now universally admitted that the fore limbs of mammals, the wings of birds, and the pectoral fins of fishes are, morphologically, merely modifications of the same organs, namely, the fore or pectoral limbs. They terminate in man in a hand, in the apes in a hand serving also as a foot, in the horse in a foot only, in birds in an organ of flight, in fish in an organ of swimming. In all these cases the function of the limbs is different, although they are morphologically identical. Furthermore, all fins are *not* morphologically identical, and if we were to attempt to regard the pectoral fins of

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fish as identical with those that occur in mammals, birds, and amphibia, because their function is similar, we should fall into serious error. It would, in the same way, be erroneous to explain the different forms of wings as they occur in mammals (bats, insectivora, and rodents) and reptiles (Draco) by referring them to the same type as the wings of birds. Although the purpose of wings is the same in all the animals named, in each individual species the organ is morphologically different; that is to say, it has originated by the adaptation to the same function of parts that have no anatomical relation. And if, from the occurrence of wings or fins in the different groups of vertebrata, we attempt to deduce a close affinity, as indicated by those

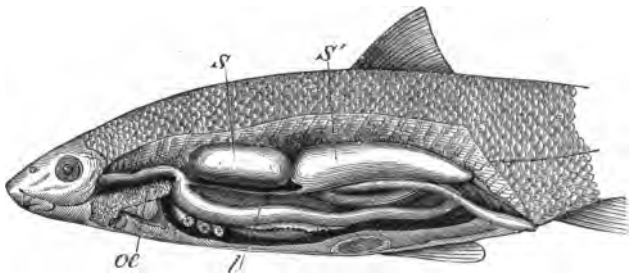

FIG. 3.—Longitudinal section of a Bleak. S. anterior; S', posterior portion of the air-bladder; œ, œsophagus; *l*, air-passage of the air-bladder.

organs, we shall indeed be gravely mistaken. We may, on the contrary, rather infer from the facts adduced that fins or wings have originated simultaneously and independently in the different groups, since different members of the body, in themselves not comparable, have, by adaptation to new conditions of existence, become such organs with similar physiological functions.

Thus, in the examples here given, wings, fins, or lungs must not be considered as hereditary characters, but merely as characters of adaptation which, as they have originated independently, are useless for determining the affinities of the animals that possess them. This conclusion is, however, only partially accurate, as shall now be shown.

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In order to do this, we will return to the more striking of the examples here given. There can certainly be no doubt of this—that the lungs of mammals have not been developed by modification from those of land snails; we know on the contrary, or will assume, that the lungs of all the Vertebrata are identical, and to be regarded as modifications of the air-bladders of the bony fishes (fig. 3), although these organs do not serve, or at any rate do not mainly serve, for respiration. On the contrary, fish breathe by their gills. But the lungs of mammals differ remarkably in structure from those of birds, and yet more from

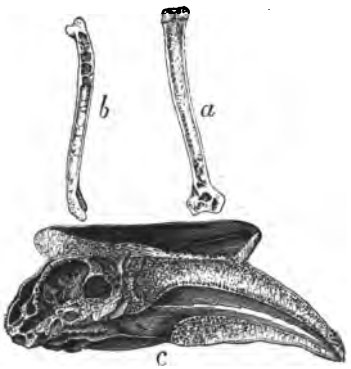

FIG. 4.—*a*, the bone of a Cat, showing the marrow-tube; *b*, that of a Bird with cavities containing air instead of marrow; *c*, the skull of a Buceros sawn through. Air-cavities traverse every part of the bone.

those of the lower reptiles or the amphibia. In these last they are usually simply capacious sacs opening into the mouth by a very short passage (the trachea); in mammals they exhibit a spongy structure, and often a highly complicated arrangement of extremely long air-tubes; in birds also the lungs have a spongy structure, and connected with them there are always numerous air-cavities which lie partly in the cavity of the body and partly, in the form of canals, deep in the bones of the skull (fig. 4) and of the vertebral column, or penetrate to the end of the extremities, forming what are known as pneumatic bones. Now these differences in the structure of the lungs of

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the different Vertebrata go hand in hand with other characters which distinguish the groups; and although we are not justified in founding the genealogies of Vertebrata exclusively on the character of the lungs, we may regard and use them as an indication of affinity, particularly when we see that the deductions from them coincide with conclusions drawn from other facts. In agreement with this we see that the peculiar

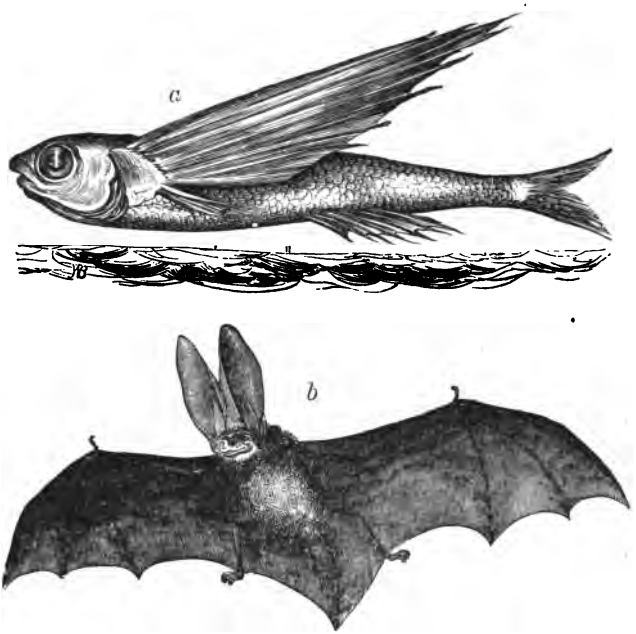

FIG. 5.—*a*, Flying-fish (*Exocetus*), in which the pectoral fins serve, at least partly, for flight; *b*, Bat, with a membrane extending between the phalanges, limbs, and tail.

construction of the lungs which in birds leads to the development of pneumatic bones is an hereditary attribute characteristic in the highest degree of the whole order of birds, and of great systematic value. It distinguishes Birds as contrasted with Mammals and Reptiles, but nevertheless can and must be conceived of as having originated through modification of a simple organ—perhaps a bladder-shaped lung—which may have been

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proper to the common ancestor of reptiles and birds alike. A similar modification of the lung might thus be found in such true reptiles as approach most nearly to birds; and in fact we see in the Chameleon (fig. 1) that long thin air-sacs, connected with the semi-spongy lungs, are suspended in the cavity of the body, and may be directly compared with the large abdominal air-sacs which are found in all birds.[1] It is evident that, by instituting such comparisons as these, we are tacitly ascribing a character to the lungs of the Vertebrata which differs from that we attributed to them when contrasting them with organs of similar physiological function in land snails and land crustaceans. For in the latter case we considered them, and with justice, not as a character inherited from the parent form, and as indicating near affinity, but as a character of adaptation, while it is only among the Vertebrata that they are of real value in estimating the degrees of affinity of the different classes. Thus it is evident that in Vertebrata they possess all the significance of hereditary characters, *i.e.* of parts which may be made use of for investigating the evolution and modification of these classes—or, as may be, orders—one from another, and for establishing such a natural system of the Vertebrata as may indicate their true affinities. The same result is obtained when the different organs of locomotion of the Vertebrata (wings, fins, legs, feet, and hands) are taken into consideration. So long as the comparison is extended to the whole cycle of the Vertebrata, these seem to have the value merely of characters of adaptation. The whale has fins as efficient as those of the sturgeon or the pike, but I doubt whether a zoologist could be found bold enough to attempt to derive the fins of the whale morphologically from those of fishes. It is quite as unlikely that anyone should undertake to prove that the wings of birds or of bats (fig. 5) could have originated by direct modification of the wing-like fins of flying fishes or of the dermal wings, supported on ribs, of the flying reptiles (*Draco*). With regard to the higher classes of the Vertebrata all these organs are, beyond a doubt, to be considered merely as characters of adaptation, and so valueless for any determination of their affinity.

But if we now turn our attention to the same organs within

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the limits of a single order or even of a single family of the Vertebrata, the case is wholly different. The wings of birds have the same typical structure throughout the whole class, and the same is true of the wings of the bats, and of the parachutes of the flying reptiles. Within the limits of these narrow groups each organ acquires a quite different value. Their constant occurrence and the similarity of their structure and development make us suppose that they must have originated through the modification of one or more simple organs in the parent form of each family. It is the same with regard to the fins of fishes, whales, and other Vertebrata. Here, as in the first example, we see that the organ or member which, within the limits of a small group, is a transmitted character, and helps in determining the affinity of the individual forms, appears as a character of adaptation when we compare the great systematic groups with one another. And choose what organ we will for this comparison, the result will be the same; parts which have little or no value as characters of adaptation assume a conspicuous diagnostic importance when we have to trace out the relations of affinity under a wide systematic aggregate, because, within the limits of the smaller groups, they may always be regarded as hereditary. Thus, too, we arrive at the conclusion that the distinction drawn, in the most recent zoology, between characters of transmission and those of adaptation, has only a partial value; for every organ which originated by adaptation, and in the first instance was worthless for the determination of the relations of affinity, may quite easily—nay, must—become transmissible by inheritance if it is rendered permanent simultaneously with improvement in other directions, in several varieties or species all derived from the same parent form. But it may be transformed into an hereditary character in a yet wider sense, particularly when an organ which has originated by adaptation in one single species, or even in one individual, is transmitted to a long series of generations which branch off into different families, though all descended from the one parent form.

It is not difficult to show by an imaginary instance how such a change in the organ might be effected side by side with permanence of the fundamental form. Suppose, for instance,

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that from the skin of one of the lower animals, say a worm, a ramified and villous prolongation arose by local excrescence which, as contrasted with the general respiration hitherto carried on by the skin, was a specially qualified organ of respiration—a true gill. This gill must be in such connection with the vessels of the body, or with the cavities which contain the circulating blood, that the absorption of oxygen by the blood may be more easily effected here than in other parts of the skin; it cannot otherwise be designated as a true gill (or branchia). But, in order to exercise the same respiratory activity as the skin, these gills must possess a certain rigidity, so that their whole surface may be in contact with the water that surrounds them, for this would be impossible to soft and pendulous gills; moreover, certain auxiliary organs must be connected with them, to secure the requisite change of water by producing a constant current. This renewal of the supply of water for respiration is frequently effected by the active movement of the branchiæ themselves, or by the constant motion of the animal; but in every case where such organs have ceased to be superficial on the skin by its induplication, or have become internal, special auxiliary organs are found, as in Crustacea for instance, Fishes, Mollusca, &c., whose sole duty is to keep up a constant stream bathing the gills. Thus the physiological efficiency of the principal organ depends not alone on the capability of the epidermal cells to absorb oxygen from the surrounding water (by osmosis), but also on those auxiliary organs which constantly supply the branchiæ with fresh water for respiration, and, by keeping up their rigidity, prevent any diminution of the respiring surface by collapse.

If furthermore we suppose that the branchiæ, which originated, perhaps, by adaptation to an increased demand on the respiratory organs, were permanent during the transmutation of the first species into several new ones, while at the same time they preserved their character of independent appendages of the outer skin, they might very likely come to act as organs not merely of respiration, but also of locomotion. For by their position, rigidity, and power of independent movement —all indispensable to their efficiency as branchiæ—they are,

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from the first, able to offer a certain resistance to the common motion of the whole body, and to serve as a fulcrum for the movements of limited sections of the body in a way that might certainly be advantageous to the whole animal. Thus a gill might be partially or wholly transformed into an organ of

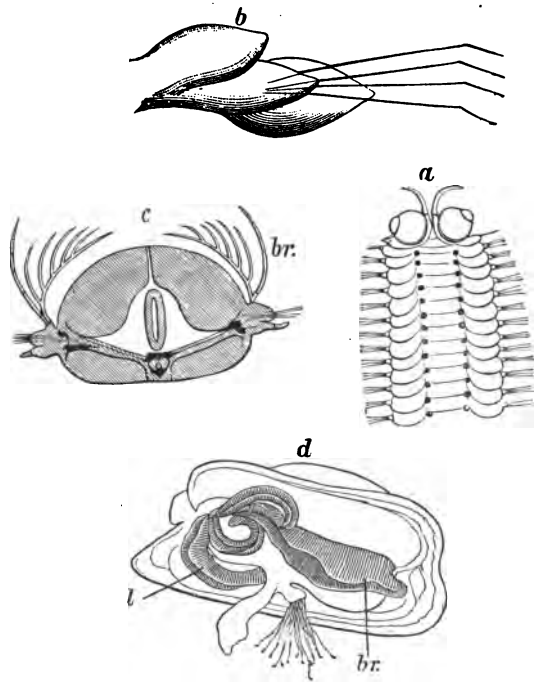

FIG. 6.—Gills, *a*, *b*, *c*, of Annelida; *d*, of a bivalve Mollusk. *a*, *Nauphanta celox* (Greeff) enlarged to three diameters, with broad gill-fins. *b*, foot of *Vunadis ornata* (Greeff), with two broad gill-fins. *c*, section of a segment of *Eunice*; *br*, the ramified gill-appendages of the rudimentary foot. *d*, *Mytilus edulis*, with *br*, the gill-folds, and *l*, the lips separated from them.

locomotion, and accordingly we find in many Annelida gill-bearing organs (fig. 6, *a*, *b*) which at the same time serve for creeping or swimming, and which present that more specialised form in which the functions of respiration and locomotion, originally exercised simultaneously by the same organ, have been

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transferred to two separate sections of the same organ, though this is still morphologically one. The branchiæ might likewise become internal, as in Fishes, Crustaceans, Molluscs, Ascidians, and so forth. The current requisite for respiration might, in such a case, be induced simply by the development of cilia on the cells of the epithelium of the branchial membrane, as occurs in all molluscs and in ascidians. The current might then serve another purpose, namely, that of bringing food to the mouth; and this is the case in the above-mentioned animals, which receive their nutrition, consisting of microscopic organisms, exclusively by the aid of the current drawn into the branchial cavity. Now, if the function of respiration were transferred by any means to some other part of the animal, or restricted to a limited section of the branchiæ themselves, the remaining portion might be transformed into an organ serving exclusively to obtain nutrition. The lips lying near to the mouth of molluscs would, in fact, appear to be such modified portions of the folds of the branchiæ.

But this is by no means the limit of such change of function. Each animal cell in the living organism is sensitive to various molecular movements which impinge on it from without. General sensibility is an attribute of the living substance of the cell. Now it would obviously be a considerable advantage to the animal that the organs of respiration or locomotion should be connected with certain organs of sense—in our example, for instance, if the lip-like appendages of the branchiæ of the molluscs could be transformed into organs of taste or touch. As every living cell, including of course the cells of the mucous membrane of the branchiæ or the labial fold, possesses this general sensibility, and this in a certain sense includes the capability for developing a special sense of touch or taste, we perceive that an epidermal member which originated as a simple gill may, by virtue of its inherent properties, easily become an organ of locomotion, sensibility, or taste, and it might equally easily be converted into an organ for the acquisition of nourishment (as in the Ascidians) or for any other purpose. At the same time be it observed, such transformations have not taken place suddenly in an abrupt and, so to speak, revo-

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lutionary manner; for their existence need not in the first instance be conditional on the introduction of new influences, since they depend on the fact that the branchiæ must from the first—or they could not have lived, grown, and exercised their functions—have contained all the elements and have exercised all the elementary functions which fitted them for differentiation in the direction indicated by those functions, and for transformation into organs apparently intended for one function only.

We arrive at the same conclusion by a simple general consideration. We know that the simplest and lowest animal, a mere gelatinous mass, say an Amœba, exercises, and must exercise, all the vital functions as well as the ovum-cell which is so rich in protoplasm, or even as the young and growing cells which constitute animal tissues—functions which in the higher animals are apparently fulfilled exclusively by special organs. The protoplasmic cell or the Amœba takes up nutrition, often indeed of a solid nature; it moves more or less quickly and voluntarily; it is sensible to impressions transmitted to it by the agitation or chemical properties of the surrounding medium; it assimilates organic matters, and breathes, inasmuch as it expires the carbonic acid formed in the process; it is capable of more or less definite sensations, for it selects the food that suits it, and it grows and multiplies often by highly complex processes. All these characters are to be found in each living protoplasmic cell of every growing organ; but it is true that it is not every cell of an organism that is in this sense living. Thus in the hair and nails, for instance, there are horny cells which no longer contain any fresh and unchanged protoplasm, and consequently can no longer grow or multiply, their increase being effected by fresh and living cells lying in the deeper skin-layers; from these, new horny cells are constantly produced and pushed forward to replace the old cells as they wear off at the angles of the nails or tips of the hairs. We may apply Brücke's expression, 'elementary organisms,' as a name for those deep-seated cells, which, being richly supplied with protoplasm and capable of multiplication, are, in the strictest sense, living cells. For as the life of every organ is the sum of the individual life of the living cells which compose it, it is clear that every living and

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growing organ, without exception, must, in a certain sense, be capable of becoming modified in any such various directions as are indicated by the common properties of the living substance of the protoplasm. The abstract and paradoxical formula for this position might be put thus:—Every living organ may, by virtue of the properties inherent in its living cells, become any other organ.

Let us now return to our starting-point. We have seen that every character of adaptation must be in a certain sense hereditary; for if those individuals of a species which first acquired any given character by adaptation were incapable of transmitting it to posterity as a part of their inherited nature—particularly if the exciting causes were to be removed—every newly acquired character would presently be lost. The inheritability of this newly acquired character might also be greatly increased if, for instance, it were transmitted through a long series of varieties or species, while at the same time it was undergoing modification. This might occur if, from the first, its fundamental character were such as must induce specialisation of its function. Now we have seen that even so highly specialised an organ as a gill is, or seems to be, must yet be capable of numerous modifications; for its primary use depended partly on other functions which were capable of further modification, *i.e.* specialisation, in a mode analogous to that by which the gill became an organ of respiration. And the more manifold the independent and latent properties are of a newly constituted organ of adaptation, the greater will the probability be that it will be transmitted by inheritance to all the divergent descendants of the parent form, and be at the same time modified to meet their altered functional requirements. But the more specialised an organ is—that is to say, the more one single purpose is developed to the prejudice of the latent functions—the harder will it be for it to adapt itself to new purposes, and so it will probably be transmitted to the descendants of the parent form but little altered. Hence it is impossible to establish an *à priori* distinction between Characters of Adaptation and Characters of Inheritance, and we perceive that most, perhaps all, of the characters now in a great measure hereditary

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originated through modifications of those originally adaptive organs which bore within them the elements of continuous and extensive gradual transformation.[2]

This inference includes another: That all the structural peculiarities of animals are true organs which must subserve some function and can never be mere useless ornaments. Otherwise, from the Darwinian point of view—which, as I have said, I accept as a standard—it would be quite unintelligible how wholly useless portions of the body could have been inherited and modified through a long series of divergent descendants from the parent form. If it could be strikingly shown that organs actually exist which are of no physiological use to the

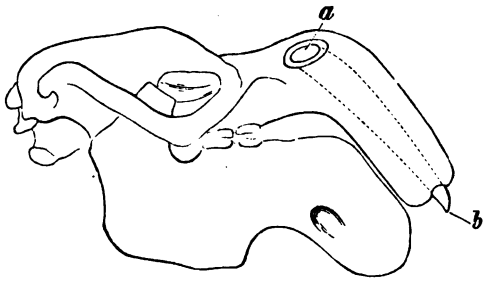

FIG. 7.—Skull of female Dugong; the colossal tusks in the upper jaw never pierce the thick fleshy lip, although they continue to grow with the jaw. *a*, the root of the tusk; *b*, the point.

possessors, but which determine the types of form in whole Classes, Orders, or Families, then the conclusion would seem inevitable that these functionless organs have been formed in accordance with some transcendental law (or plan) of development.

Now it is sometimes asserted, oftener, it is true, by botanists than by zoologists, that such functionless organs do in fact exist. I do not here allude to rudimentary organs;[3] for although these appear in sundry groups of animals to be in fact devoid of any recognisable function, they are derived, no doubt by degeneration, from true organs whose functions are conspicuous in other animals. The best example known to me of such rudimentary organs is offered by the female Dugong (*Halicore*

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Dugong). This creature has enormous tusks which continue to grow as the animal grows, and are even larger in proportion in the adult than in the young. Thus the tusks of the female grow more quickly than the skull. They are nevertheless wholly functionless in the female; that is to say, they are used neither as tusks nor as teeth, for they are completely encased in the upper jaw-bone, and the blunt point is covered by a huge fleshy upper lip forming a snout. The male Dugong uses his tusks, which project at the sides of the mouth, as weapons or for other purposes, as is proved by the fact that the outer surface of the points of the tusks is, without exception, much worn in every male skull found in our collections. The tusks of the female Dugong are rudimentary and functionless as teeth; however, like all similar rudimentary organs, they are not included in the above-mentioned class of functionless organs, which, in spite of their immense variety and often conspicuous size, cannot be regarded either as true organs now exercising their functions, or even as true organs in a degraded condition, such as are known in scientific parlance as 'morphological characters,' in contradistinction to 'physiological characters,' that is to say, those whose use is obvious or well-known. The existence of such morphological characters has been affirmed, as I have said, even of animals; but it still seems doubtful whether those organs and parts of the animal body which we include in this category do in fact belong to it, and are not perhaps thus classed merely because as yet we know nothing of their functional importance. Even when we assign to such parts the smallest possible importance in the life of the animal, we ought not to forget that they consist of living cells, or are directly dependent on them. Hence we are justified in propounding the thesis that every part which we are accustomed, from its lack of conspicuous physiological character, to regard as a morphological character, must nevertheless have a certain functional value in the general economy of the animal, since it must produce a fraction, however small, of the material which is formed in the living body, and must possess a proportionate share of all its properties.

At the same time it cannot be disputed that even in

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animals, though certainly less often than in plants, peculiarities of structure do occur which appear to be absolutely useless to the life of the individual, although they are not rudimentary organs. Such, for instance, are the colours of the skin of many, and especially of marine, animals; many expansions of the skin and the sculptured character of the skin of Reptiles, Crustaceans, and Insects would seem to be of this nature; the relative positions of the various organs, which may sometimes be said to be highly inappropriate, the number of the extremities in various animals, and many other circumstances also come under this head. It would be a highly important task for a zoologist, and, I believe, fertile in results, to discuss all these cases in detail, in order to see whether, or how far, our present knowledge suffices to explain them; *i.e.* to show that such morphological characters do not in fact exist in animals. In this place it must suffice to discuss one single example.

It is known that the skin of Reptiles encloses the body with scales. These scales are distinguished by very various sculpturings, highly characteristic of the different species. Irrespective of their systematic significance they appear to be of no value in the life of the animal; indeed they are viewed as ornamental, without regard to the fact that they are microscopic and much too delicate to be visible to other animals of their own species. It might therefore seem hopeless to show the necessity for their existence on Darwinian principles, and to prove that they are physiologically active organs. Nevertheless recent investigations on this point have furnished evidence that this is possible.

It is known that many Reptiles, and above all the snakes, cast off the whole skin at once, whereas human beings do so by degrees. If by any accident they are prevented doing so, they infallibly die, because the old skin has grown so tough and hard that it hinders the increase in volume which is inseparable from the growth of the animal. The casting of the skin is induced by the formation, on the surface of the inner epidermis, of a layer of very fine and equally distributed hairs, which evidently serve the purpose of mechanically raising the old skin by their rigidity and position. These hairs, then, may be designated as *casting hairs*. That they are destined and

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calculated for this end is evident to me from the fact established by Dr. Braun that the casting of the shells of river Cray-fish is induced in exactly the same manner by the formation of a coating of hairs which mechanically loosens the old skin or

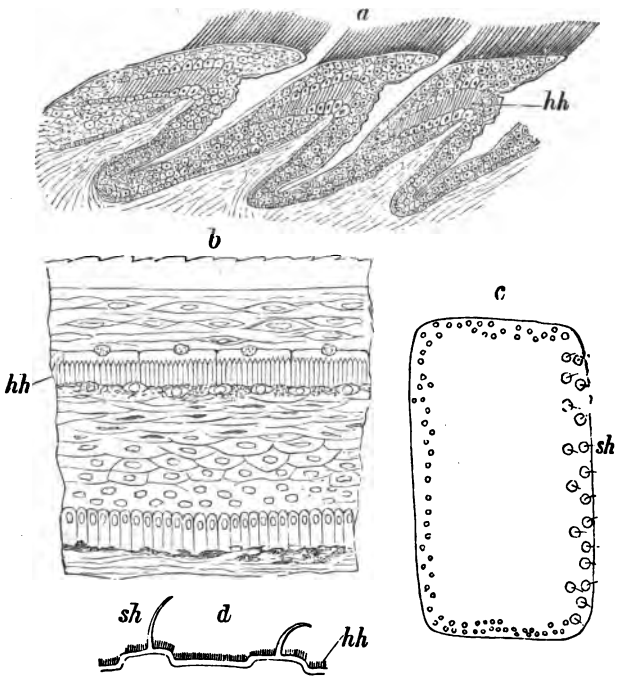

FIG. 8.—Casting process in the skin of reptiles. *a*, in the clinging bristles of the foot of the Gecko; within the epidermis are seen the casting hairs, *hh*, destined to form the new clinging bristles. *b*, in the Adder; *hh*, the casting hairs; the portion of skin above them is pushed away, and the hairs themselves form the ridges on the new skin. *c*, a scale of *Phyllodactylus*, with the little sensitive hairs *sh* at the right edge. *d*, *Thecadactylus*; *sh*, the sensitive hairs; and *hh*, the casting hairs which do not change during casting. From Cartier.

shell from the new. Now the investigations of Braun and Cartier have shown that these casting hairs—which serve the same purpose in two groups of animals so far apart in the systematic scale—after the casting are partly transformed into the concentric stripes, sharp spikes, ridges, or warts which

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ornament the outer edges of the skin-scales of reptiles or the carapace of crabs. Hence we are justified in regarding the sculpture thus produced on the epidermis of these animals as a rudimentary organ; for the microscopic casting hairs, after they have done their duty in inducing the casting, remain where they were formed, somewhat altered in form, it is true, and without any further visible use.

Occasionally, however, these hairs, after they have fulfilled their office, are transformed into organs which are capable of serving other useful purposes to the reptile. Thus, for instance, Von Leydig discovered certain organs in the skin of reptiles, which he designated as organs of a sixth sense, regularly communicating with long elastic hairs which project far above

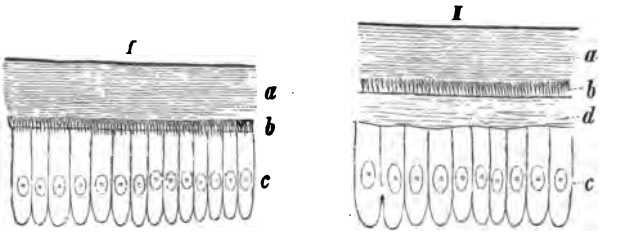

FIG. 9.—Stages of casting in the carapace of the freshwater Cray-fish, from Braun. I. First stage; *a*, the two old cuticular layers; *b*, the layer of casting hairs; *c*, the epidermis cells. II. Second stage; *a*, *b*, *c*, as in I.; between *b* and *c* the new cuticle *d* has intervened.

the surface of the skin, and seem admirably adapted to transmit every impact or molecular movement to the sensitive and guiding organs that are connected with them. These sensitive hairs belong to those casting hairs just mentioned, of which some few, that are placed in suitable positions, have been transformed into such sensitive hair-organs (fig. 8, *sh*). Many of the teeth and ridges which are formed on the surface of the scales by the coalescence of casting hairs are so placed as to be of use in the difficult process of stripping off the whole skin on whose surface they are situated, for they serve as holdfasts to the rough surface of stones. Another still more striking example is exhibited by the family of the Geckos, which are all distinguished by having an immense number of long stiff movable

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bristles on the soles of their feet, which give these creatures their well-known power of running with great rapidity along vertical walls or the ceiling of a room back downwards, without falling.[4] These hairs, like those described above, are nothing more than specially developed casting hairs, for they originate in the same

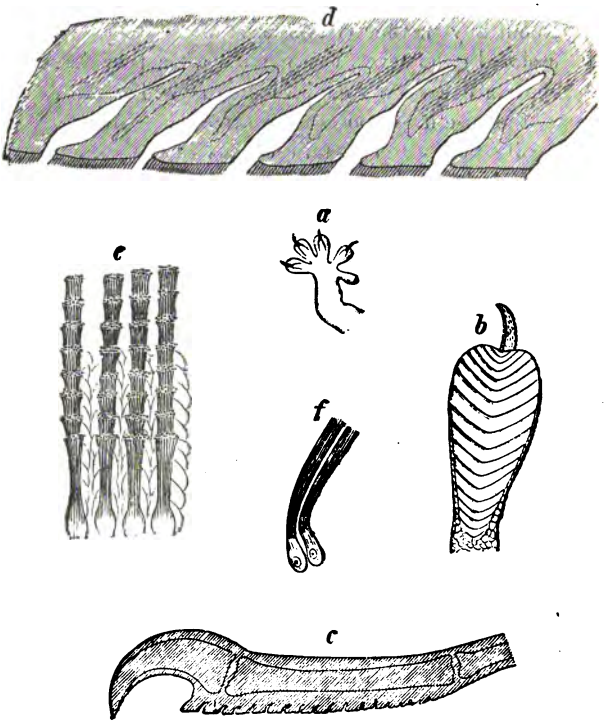

FIG. 10.—Structure of the Gecko's foot; *a*, from above; *b*, a toe with its clinging ridges, from below, slightly magnified; *c*, diagram of section through a toe, exhibiting the ridges in section; *d*, a few of these, magnified, with their bristles; *e*, four rows of bristle-cells, much magnified; *f*, two separate bristle-cells, more magnified. From Cartier.

way as those, and assist in the process of casting (fig. 8, *a*). The clinging hairs are absent in the embryo of the Gecko; they do not appear till the first casting, and assist in causing the process; this sufficiently proves that they were not primarily destined to be used as organs for clinging, but have acquired

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that use after first serving their other function. The sculptured patterns on the scales of reptiles, on the other hand, may be regarded as the transformed and now useless remains of those casting hairs whose utility ended with the preparing the old dead skin for its casting by slightly loosening it; while the remains of others of these casting hairs have grown to be other functional organs—as sensitive hairs and clinging bristles—because they possessed such characters as qualified them for such special functions. Hence we may say that the sculptured markings on the scales of those reptiles which cast their skins are no longer to be designated as morphological characters, since it has been shown that they originate by the transformation of parts which have a determinate, highly specialised and indispensable, or at any rate most useful function to perform in the life of the animal.

This one example may, and in this place must, suffice to show that we need not abandon the hope of explaining morphological characters on Darwinian principles, though their nature is no doubt often difficult to understand. If it be granted that it is possible—or if we are at any rate allowed to attempt—to show, that in fact all those hitherto inexplicable and so-called morphological characters have still a determinate function, or have at any time had one, and may be regarded as true or as rudimentary organs which were enabled by their living elements to undergo further transformations and changes of function—if so much as this is hypothetically granted, the direction of our researches is clearly pointed out, and we are justified in prosecuting them. For since we consider *all* the parts of the animal body as true organs, and see that the sum total of their functional activity determines the vital fitness of the species, we perceive that it is the task of the zoologist to enquire how the conditions of life must act upon individual animals and their organs, in order to be able to deduce our inferences as to the physiological causes of the origin of different animal forms. We shall not, however, follow the morphologist, who seeks to trace the affinities which must exist between all living animals by investigating and comparing the forms and organs of living and extinct animals as well as the

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processes of their development from the egg. For although the morphological section of animal biology teaches with much probability that this species or that organ has undergone this or that course of modification in the animal series, and that in the process of modification it has passed through a whole series of various forms, still it is only physiological research that can elucidate the necessity for their existence by revealing their causative conditions.

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SECTION I.

GENERAL PRELIMINARY CONSIDERATIONS.

CHAPTER I.

THE PHYSIOLOGY OF ORGANISMS.

THE general direction of zoology is, as we have seen in the introduction, determined by two branches of science—Morphology and Physiology. Although both make it their task to learn to understand the phenomena presented to us by the animal kingdom, they are so widely different, both as to their details and as to the paths they have struck out for solving the problems, that we are fully justified in keeping them separate as two independent branches of science.

The problem for Morphology is to discover those affinities of relationship in animals which actually exist, and to found on them a natural system of the animal kingdom. It attains this end, or endeavours to attain it, by investigating morphological differences, as well as those similarities which indicate a true affinity, by means of the comparative method—comparative anatomy and embryology. Physiology, on the other hand, does not seek to establish those affinities, but, on the contrary, to investigate those universal conditions of existence and those functions of living organisms which may elucidate from the point of view of the laws of causation, among other things, the natural system arrived at from morphology. Morphology, indeed, only establishes the relations of affinity between individual

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species; if it ever should succeed in finding a truly natural system corresponding to these relations, this in itself would be the best morphological evidence of the accuracy of one of the principal propositions of the Darwinian theory, *i.e.* of the genealogical relationship of all animals. But Physiology, taking this result for granted as a fact, endeavours to explain it by revealing its physiological necessity, *i.e.* its dependence on external and internal causes whose united action has, slowly or rapidly, caused the transmutation of one animal form into another.

It will be advisable to illustrate this proposition by shortly discussing an example. Morphology teaches us that two pairs of organs of locomotion—limbs—are a marked characteristic of the Vertebrata, and that two pairs only do not occur in any other animal group. Moreover, we have learned that these two pairs of extremities must have possessed the highest degree of plasticity, since they are found, throughout the vertebrate series, of the utmost variety of form and structure; while at the same time their variations are so characteristic that they furnish us with an easy means of tracing even very close relations of affinity between different animals. But Physiology has hitherto been wholly unable to detect the causes which led to the development of only two pairs of limbs in the Vertebrata; since no self-evident usefulness can be directly ascribed to the exact number of four organs of locomotion, and it is undeniable that many vertebrate animals could move just as well with six or more legs as with four; there are fishes, too, as the Eel, which are wholly devoid of them, and yet move forward with great rapidity by a wriggling motion of the body; and Snakes, which have not four legs either, run, as is well known, with extreme rapidity on the points of their numerous ribs. To find a reason for the prevalence of four limbs in the Vertebrata, and at the same time the cause of their origin, is precisely a problem for Physiology. Even if an invertebrate animal were to be found, which, on general grounds, might be regarded as the nearest invertebrate ally of the Vertebrata, and which, moreover, in its larva or embryo stage exhibited organs which in position and structure might be regarded as comparable with the simplest of

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the four typical organs of locomotion of the Vertebrata, such a discovery would indeed be hailed with delight by the morphologist.[5] But the physiological problem would remain unsolved; it would merely be transferred from the Vertebrata as a class to that group to which this hypothetical animal might belong. From the most general point of view the purely physiological problem is, to say the least, of just as much importance as the morphological.

After this illustration we may set morphology wholly aside, and pass on to a general preliminary consideration of the subject of the present volume, *i.e.* the 'General Physiology of the Animal Kingdom,' or, as I first named it, the Physiology of Animal Organisms—a title by which I intended to convey a certain opposition or contradistinction of the subject of which it treats to the general conception of Animal or Human Physiology.

Everyone is aware that the science which is usually known simply as Physiology endeavours almost exclusively to explain the functions of different organs, and is not unfrequently confined within even narrower limits, in accordance with the assertion of a well-known German physiologist, that this science is useful only or principally in practical medicine, and must be regarded as subservient to it. This familiar form of physiology is merely the physiology of the organs; its aim is to verify the laws by which the organs of sense—such as the brain—the muscles, stomach, heart, spinal cord, lungs, kidneys—in short, each of the various organs—exercise their functions. I am, I need not say, far from disputing the immense value of this branch of study, or even from thinking that its results can ever be disregarded by the zoologist. I nevertheless must maintain that another field, as yet almost unworked, lies open to physiological enquiry—nay, more, that organic physiology has not afforded such assistance to zoology as it might have done if it had been less exclusively forced into the service of practical medicine. An immense number of questions bearing the highest general scientific importance lie open to physiological enquiry in the vast number of different species of animals; but they are never, or but rarely, answered or even worked out, for

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they cannot be solved by the few animal forms on which physiology is wont to make her experiments. It is certainly no exaggeration to say that not more than six or eight—at most twelve—kinds of animals from among the many thousand existing forms, have hitherto been investigated by physiology as it is understood in our universities.

But even supposing that the laws of organic physiology had been deduced from the investigation of the greater number of living animals instead of merely a few, it still could not avail to answer the questions which arise from the reciprocal relations of animals, and which bear upon the external conditions of existence. But these, above all others, are those that claim our interest, if our point is to establish the most universal laws of the development of organisms and of the transmutation of one form into others.

In order to set this in a clear light, I think it will be advisable to compare, in the most general manner, two groups of facts which apparently have no common point of coincidence —the geographical distribution of animals, and the normal arrangement and functions of organs in the individual animal.

All the organs of an animal are in co-ordination, physiologically as well as morphologically. Although the liver and blood-vessels, brain and muscles, and all the organs appear to act independently of each other, they are so absolutely dependent on each other that they are wholly incapable of doing their duty as soon as their relations, sometimes very remote, to the other organs are interrupted. Thus the muscles of the arm, though the arm itself were uninjured, would cease to act with any purpose if they were made independent of a healthy will; and this again depends on the normal activity of our vascular system, for if the blood-vessels of the brain are excessively or insufficiently supplied the functional activity of the will must suffer. And every separate organ is in the same way influenced, and its activity determined, by others, or by all the rest. If one organ is in any degree changed, every other will be affected and changed more or less.

The same law applies in a certain measure to the present distribution of animals on the surface of our globe. It is, no

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doubt, evident that the animals now inhabiting Australia are so widely separated from those of England that, irrespective of other circumstances, it would be quite impossible for them to have any influence on each other. But if we turn our attention to a defined region, such as North or South America, where the most widely different animals live in the most intimate and ever varying contiguity to each other and to the plants which occur there, the case is altogether different. If the American prairies were to cease to produce grass, the first result would be the rapid and utter extinction of the now numerous herds of buffaloes, and on their existence depends that of the surviving remnant of the ancient Indian population of America. If the various insectivorous birds of North America were exterminated, within a very few years beyond a doubt all the produce of the rich agricultural districts of that continent would be destroyed. If we change the mode of life of any single animal, the change will instantly have an influence on all the other animals whose healthy existence was in any way dependent on its normal function before it was altered. Although it is certainly true that the various animals inhabiting a country are not so intimately interdependent as the organs of the individual, the relations in the two cases may be very directly compared. The normal numerical proportion, mode of life, and distribution of animals would be altered or destroyed by the extermination of one single animal, just as the whole body suffers, with all its organs, if only one of them is destroyed or injured. And in both cases nature has analogous remedies at her command. In the one case the function of the incapacitated organ can be assumed, at any rate to a certain extent, by some other uninjured organ, exactly as, in the other case, the function of the exterminated animal may be fulfilled with regard to the whole fauna of the country by some other animal. But a perfect compensation for the loss sustained is impossible in either case.

This parallel between an individual organism and the conditions of distribution at present existing may be carried out with reference to the purely morphological relations.

Every animal body is constructed to a certain extent in

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accordance with a determined type, and every individual of a species repeats the organisation of its parents without any considerable or abnormal deviation from it. And it is well known that this is the case not only with reference to the mere existence or reproduction of the same organs, but with regard,

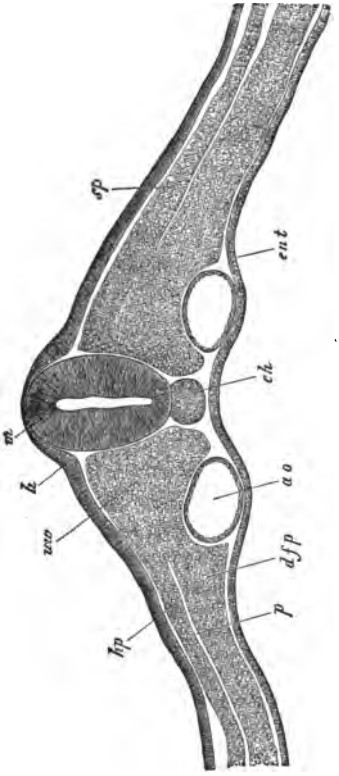

FIG. 11.—Germinal layers of the Chick, from Kölliker. Section of the young embryo, showing the first (germinal) layer from which the organs originate by gradually increasing differentiation.

above all, to their position. This topography of the organs of an animal is, to say the least, of quite equal significance with the existence of the individual organs; so much so that the development of our modern views as to the embryology of animals—the history of their individual growth—rests essen-

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tially on the axiom that the topographical relations of the individual organs must always be of the same general type, notwithstanding the utmost variety in the forms of the organs themselves or of the animals to which they belong, so long as these are included in the same systematic group. Thus, for instance, a vertebrate animal with a brain in the foot, as sometimes occurs in Mollusca, or with an ear in its tail, as in certain Crustaceans, is simply an impossibility; among the Vertebrata these organs are always necessarily located in the skull, or brain-capsule, which is invariably in the head; every organ, even the most insignificant, as it might appear, has its determined position from which it is but rarely displaced. This topography or distribution of the organs is indicated and recognisable at a very early period in the life of the individual. Before any kind of organ is constructed and adapted to any determined use, two or three embryonic layers or strata of cells are formed (fig. 11), known to embryologists as the germinal layers. Each of these is gradually formed or differentiated into certain organs. Thus, for instance, it is now ascertained that the central nerve-system originates in almost all animals directly from the outer layer, the so-called 'Ectoderm,' of the embryo; and we know also that the eyes and ears are formed in the same way from this outer germinal layer, and at the same time from the central nervous system, which has been already separated from it. The same obtains of all the other organs, of which some always originate from the inner germinal layer, others again as invariably from the median layer. This stratification of the body, which is, on the whole, tolerably uniform in all animals, and the early appearance of the three principal germinal layers, can no longer be doubted.

If we now look at a map of the world on which the distribution of the fauna into districts is indicated by different colours, and compare this with the lists of Birds, Mammalia, or Reptiles which usually accompany such a map, we perceive that a great number of species, genera, and even families occur in only one district and not at all in the others. This matter has lately been admirably treated by the distinguished English naturalist Wallace, whose work on the geographical distribution

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of animals will long be the chief book of reference for all who take an interest in the subject. I would refer the reader to Wallace's book, and think I may therefore fairly refrain from adducing numerous instances to prove that in the present distribution of animals on the globe an equally sharp demarcation of the stratification of the groups of animals can be discerned as of the topography of the organs in an individual organism. No one will expect to find living Marsupials in England or Germany, or buffaloes, stags, and other Ruminants in Australia. The reader who is acquainted with Wallace's work on the contrast between the faunas of the Australian and Indo-Malayan provinces will not have been surprised—on the contrary will have felt a certain satisfaction—at hearing that an animal has lately been discovered in New Guinea belonging to the group of the Monotremata and nearly allied to the Ornithorhynchus.

If we could describe the embryology of these groups of fauna —*i.e.* if we were in a position to represent the development of each distinct fauna from the earliest geological periods down to our own time with anything approaching to the same completeness as we can now attain with regard to the embryology of many animals—we should undoubtedly be able to trace the present distribution of animals up to very remote geological periods. The brilliant results, far transcending all that had been previously achieved, of the palæontological investigations in North America by the American naturalists, who annually risk their lives to obtain scientific results, will undoubtedly ere long put them in a position to give us an almost complete history of the secular evolution of the North American fauna; and I am convinced that the elucidation of this branch of natural history will not only reveal many more important intermediate forms between different vertebrate types than are now known, but also that the main features of the present distribution of the North American Vertebrata will be recognisable in that of the fossil fauna, precisely as the general arrangement of the organs, in which the most dissimilar animals agree, is indicated from the first in the primary germinal layers.

Enough has been said, I hope, to prove that we are justified

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in comparing the organs of the individual, their action and their distribution, with the different species of animals, and their present distribution and functions on the globe. The fauna of a district thus takes the aspect of a vast organism whose separate members—the different species of animals—are living parts of the body, and which has had too its embryology, *i.e.* its development in time. These species, as regards the laws of their local distribution, may be regarded *morphologically* as the limbs of a gigantic organism which throws one or another of them up into the air on to the top of some mountain peak, while others are flung into ocean depths, subterranean caves, lakes, or rivers. But they may also be studied *physiologically*, and compared to organs which by their functions and importance influence the life of the whole mass, and are interdependent by the most various physiological relations, like the organs of a healthy living organism.

It is in agreement with these arguments that we apply the expression 'Universal Physiology,' or 'the Physiology of *Organisms*,' in contradistinction to the Physiology of *Organs*, to that branch of animal biology which regards the species of animals as actualities and investigates the reciprocal relations which adjust the balance between the existence of any species and the natural, external conditions of its existence, in the widest sense of the term. Each separate organ, even when influenced by other parts of the body, must exercise its own specific function. The sum, or, to speak more accurately, the resultant, of all the forces simultaneously at work in an individual, constitutes its individual life; and its general well-being and its capability for maintaining the place it has once acquired in the struggle for existence are the result of a combination of the numerous different and often antagonistic functions of the individual organs. This is equally true of species, if we regard them as members of a single vast organism; and this organism can only maintain its place in existence —the distribution, that is, of its members on the surface of the earth—by the efficient action of its functions, *i.e.* by the reciprocal activity of the species which constitute it, sometimes

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co-operative and sometimes antagonistic, sometimes under the influence of the external conditions of life and sometimes opposed to them.

Under the term 'Physiology of *Organisms*' we may therefore comprehend all those laws which are known to us from the investigation of the relations of various species to each other and to those conditions of life which maintain, destroy, or modify their existence as species. Special physiology, on the other hand—which in its present stage is often termed simply human physiology—or, more accurately, the 'Physiology of *organs*,' includes all those facts and laws which refer chiefly or exclusively to the specific action or re-action of the organs of individuals.

The subject-matter of the following chapters has now been exactly enough defined. We shall leave the laws of the relations of affinity as revealed by morphology entirely out of the question, accepting them as they stand, without criticism. In the province of physiology we shall in the same way disregard, as far as possible, the physiology of organs; for, at any rate in the first instance, it is of no importance to our more general problem that the use of each organ should be determined. The interest of these specific enquiries extends only so far as they may be of value in determining for a species its capability of existence as such. At the same time it must never be forgotten that the results of the more general enquiry can never contradict the really well-founded facts and laws of special physiology, and we shall consequently be obliged again and again to refer to them, especially when a species depends principally or exclusively on the healthy and vigorous action of its organs for the possibility of maintaining its place in the struggle for existence.

Before going on to this particular enquiry it seems desirable that the expression 'External Conditions of Existence' should be as accurately defined as may be. I have already said that I wish to see as wide an application given to it as possible, so as to include every influence, however insignificant and difficult to detect, that can affect the 'fitness for survival' of a species, and to investigate its mode of action. This explanation might

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suffice, but I prefer to illustrate my meaning by a few further considerations.

Everything which tends to hinder or to favour the continuance of the life of the individual and the propagation of the species, as such, must be regarded as a condition of existence for that species. In this sense every organism existing on the face of the globe, as well as every inorganic constituent of the earth's surface and of the atmosphere, is a condition of existence for all animals. Their relations to those organic and inorganic elements differ only in degree, in being more or less remote. Heat or cold, light as well as nourishment, the density of the atmosphere, the water or the soil in or on which animals pass their lives, electricity and the chemical constituents of the media surrounding them, whether air or water, the plants or other animals with which they live, either in the closest connection or in mere association—everything, in short—may and must exercise a certain influence on animals, and may be harmful or prejudicial to them; and there is nothing on the face of the earth that may not be regarded as an essential condition of existence to some species of animal. It is self-evident that the influences of these manifold conditions must be in the highest degree various. One animal requires a high temperature in order to live, another a low one; one form prefers a very damp atmosphere, another a dry one; many are destined to live always under water or in the soil, while quite as many disport themselves in the freer medium of the air. If we could suddenly reverse all the conditions of existence which are indicated by these modes of life, we should annihilate all the animal life on the earth; for no fish can swim in the air, no bird can live permanently under water, a mole cannot climb, a salamander cannot exist in a desert, nor a desert-snail in the virgin forests of the tropics. If, on the contrary, we reverse the conditions slowly, but still at a perceptible rate, it is probable that most animals would perish while a few would survive. But if we suppose that such changes —in the atmosphere, for instance, in the constituents of water or of the soil, &c.—were effected so slowly as to be perfectly inappreciable by man, it is highly probable that the number of surviving forms would be very considerable. The influence of the

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conditions of existence thus changed is sometimes very different on nearly allied forms; for instance, one species of Neritina can live equally well in fresh, brackish, and sea water, while others occur only in one or the other, and cannot survive any diminution or increase of the saltness of the water they live in. The simple reason of this phenomenon is the fact that the life of an animal depends not merely on the influence of the external conditions, but on the reaction of its own organisation. If we transfer a stickleback (*Gasterosteus aculeatus*) directly from fresh to salt water, and leave it there for days or weeks, it will not perish if it is supplied with sufficient food. But if at the same time we place one of the common fresh-water mussels (*Unio* or *Anodonta*) in sea-water it will soon die, sometimes in a few hours. The remarkable difference in the behaviour of these two creatures is easily explained by the following hypothesis: In both animals the salt water is transmitted through the skin to the tissues of the body; but this takes place to a much greater extent in the mussel than in the fish, and thus injures it, while the fish can bear the small quantity of salt it has absorbed. If our migratory fishes, as the salmon, had as great an affinity for the salt of the sea-water as the mussels have, they would soon cease to exist, or would have to become adapted to live wholly in fresh water. Thus every change in the conditions of existence influences different animals in different ways. The problem, then, is to investigate more accurately these different effects of changed conditions.

If we suppose that some such secular change in the conditions has been effected, or that certain animals have in some way or other been transferred from their original stations into other circumstances, the effects of such a change in either case may be the same or quite distinct; and this in two ways. It might occur, in the first place, that, the whole species not having perished under the new conditions of existence, a certain kind of selection was made among the survivors, as in the above-mentioned instance of the fresh-water mussel and the stickleback. This selective power, however, may be exerted not merely on a species as a whole, but on the more or less dissimilar individuals that compose it, and even on the organs

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of each individual. An organ exclusively adapted to a certain medium, or fitted only for one restricted use, must degenerate and at last disappear if it becomes useless by the change of conditions, even though the animal itself does not suffer from this on the whole. Or, secondly, the animal, though not exterminated, may be more or less crippled or altered. An organ no longer needed for its original purpose may adapt itself to the altered circumstances, and alter correspondingly if it contains within itself, as I have explained above, the elements of such a change. Then the influence exerted by the changed conditions will be *transforming*, not *selective*.

This last view may seem somewhat bold to those readers who know that Darwin, in his theory of selection, has almost entirely set aside the direct transforming influence of external circumstances. Yet he seems latterly to be disposed to admit that he had undervalued the transforming as well as the selective influence of external conditions; and it seems to me that his objection to the idea of such an influence rested essentially on the method of his argument, which seemed indispensable for setting his theory of selection and his hypothesis as to the transformation of species in a clear light and on a firm footing. By a rearrangement of the materials of his argument, however, we obtain, as I conceive, convincing proof that external conditions can exert not only a very powerful selective influence, but a transforming one as well, although it must be the more limited of the two. We shall presently see that in many individual cases direct effects of this kind have been actually observed and perfectly established by a systematic series of experiments. The discussion of these must naturally be reserved for the chapters to which they belong.

Finally, I have yet a few words to say on another objection which has already been frequently made to the view which is here brought forward. It is pretty generally supposed—and indeed the facts often seem to bear it out[6]—that those changes of organs or of organisms which are brought about by the direct influence of any external cause are neither constant nor hereditary, so that the varieties that have originated in such a manner seem incapable of any share in the process of trans-

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forming one species into another; for every subsequent change in the conditions of existence would give rise to fresh changes, of advance or retrogression, so that it would become impossible for them to develope any further in one particular direction. Under such a theory as this it would evidently be quite superfluous to investigate the influence of outer circumstances on animals and on their organs and mode of life.

But this objection rests, as it seems to me, on the false assumption that the external conditions are constantly and rapidly altering, so that each variation caused by them is counteracted at once by some antagonistic external influence. This assumption is, as we know, in direct contradiction to the fact that the external conditions in reality remain constant through extraordinarily long secular periods. Thus the assumption would seem well-founded, that animals might be acted upon merely by the constant, uniform repetition of certain influences,[7] and strongly enough affected to become capable of maintaining the characters thus acquired, even when the external causes which gave rise to them were removed by some fresh change. Hence it is impossible in our enquiry to ignore the transforming influence of the conditions of existence, merely in order to fall in with a somewhat commonly accepted dogma; for it is only by assuming that such effects are possible, and directing our enquiries and experiments accordingly, that we shall be able to arrive at any decision on the question whether such transforming influences have played any part in the development of animal types or not.

After these somewhat long, but indispensable, general considerations, I must briefly indicate the classification and arrangement of the material which was best fitted to elucidate the study of the action of external conditions on animal life. At first sight it might seem that it would be well to distinguish the Transforming from the Selective influences. Such a classification would, however, involve us in many inconveniences. In the first place the two divisions would be widely different in extent; for while we have no particularly rich store of experimentally grounded facts, even with regard to the selective influences of external conditions, with regard to direct trans-

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forming influences we have next to none. I therefore prefer to adopt an apparently arbitrary and illogical division, classing the external influences as (*a*) those that belong to inorganic or inanimate nature, and (*b*) those which are due to living organisms, and above all to living animals of other species. To the first class naturally belong all the relations which originate in the need of animals for inorganic nourishment; and this, though it is not unfrequently consumed in the form of living animals, is not able to exert its specific influence until they are dead.

This division is, as I have observed, somewhat illogical. But, irrespective of the impossibility, at present, of adopting any other, it has this advantage—that it indicates at once the fundamental differences between the two groups. The influences of the first group may be both selective and transforming, while those of the second are exclusively selective. However, this division is not altogether sharp and accurate, as will be seen.

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SECTION II.

THE INFLUENCE OF INANIMATE SURROUNDINGS.

CHAPTER II.

FOOD AND ITS INFLUENCE.

The necessity of nourishment.—It is universally known that most animals begin their existence as very minute, often indeed microscopic, elementary bodies, as eggs which are simply cells and usually immeasurably smaller than the parent animal. This disparity of size is most marked among the mammalia, the most highly developed group of the animal kingdom; the ovum cell being always microscopically small, while the animals are often of gigantic size. This difference of size shows, without any further proof, that in most cases the nutriment present in the ovum must receive further additions of organic matter [8] to enable the animal to acquire its proper size; and as animals cannot, like plants, form these matters themselves by the decomposition of carbonic acid, they must take it up from external sources in the form of ready elaborated organic tissues—which is equivalent to saying that animals must derive the organic portion of their nutriment from other organisms. The need of the growing animal for such organic nourishment is, as we well know, very great.

But this imperative need of constantly adding new supplies of organic matter during the period of growth to the nutriment which the young animal has derived from the egg is not the only cause which obliges it to be always seeking nourishment;

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there is a second, which in later life is at least equally pressing. If there were no other cause, the animal might cease to eat as soon as it had attained its full growth. But everyone knows that regular and, in some cases, numerous meals are required, and consequently every animal is forced, to the very last day of its existence, to seek food, although growth has long since ceased. The reason for this is very simple. That sum of functional activity which we call life can only be maintained by using up the organic matter contained in the tissues of the living body. The activity of the muscles and of the brain, the sensitiveness of the sense-organs to external impressions, the secretion of urine or perspiration, respiration, propagation, and the assimilation of food—in short, all the vital processes that are carried on in the living individual—are only possible through the consumption, or, more correctly, the decomposition, of a corresponding amount of the organic matters contained in the organs that are exercised. The minimum of matter thus destroyed may be greater or less in different animals, sometimes even inappreciably small; but the loss of even this minimum of organic matter must sooner or later endanger the life of the animal if it is not soon made good. In order to make it good and to be at the same time in a position to carry on uninterruptedly the normal process of loss of its own tissues by secretion, the animal must consume nourishment in various proportions according to its needs. There are apparent exceptions to this rule: for instance, the well-known cases of animals—Amphibia, Mollusca, and others—which are able to live for years without food. I myself kept various species of land-snails for years wrapped in paper and quite dry in wooden boxes, and thus wholly without food, and many of them are at this day alive and active.[9] The explanation of this striking instance is easily found. The amount of nourishment required daily by any animal must naturally be equivalent to the organic matter which is daily used up in the various organs to keep up the vital processes: the more active an animal is, the more food will it require. But the vital processes of animals that are as low in the scale as the Amphibia or Univalves are extremely feeble; their respiration, even under the agitating influence of pro-

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pagation, is not sufficiently energetic to raise the temperature of the body perceptibly higher than that of the surrounding medium, whether air or water. In such animals the need for food may be in fact suspended for a long period, as their vital processes can easily be reduced to a minimum without endangering life. But, notwithstanding the privation of nutrition, a certain consumption of organic constituents, however small, must be constantly going on; for such a consumption is inseparable from respiration, and this, even when reduced to the lowest point, can never be wholly suspended without endangering the life of the animal. Thus, in such cases, the cessation of consumption of nutriment in no way proves that the animal could have carried on an active life without food, but only that its vital activity can be to a certain extent latent for a long series of years; still, not for all eternity; on the contrary it is perfectly certain that, even in an apparently latent life, a certain consumption of organic tissues goes on, since without it respiration, which is indispensable even when reduced to the lowest point, is impossible, and so death must ensue even with those animals that have the utmost powers of resistance. Thus distinctions can only properly be made between the difference in the amount consumed and the greater or less resisting power as affected by that difference. Thus, for instance, warm-blooded animals generally can scarcely live a week without food, while cold-blooded animals can often support life for many months without nourishment; and it is extremely interesting to observe that animals so high in the scale as the Mammals that hybernate can, in the same way, carry on a latent life for months without any nourishment, like Land-snails or Amphibia; not only do they not suffer, but they actually require this period of negative existence during their winter sleep for the maintenance of their normal vitality. For certain reasons to be discussed presently, these animals during their hybernation have been compared, and apparently with justice, to the cold-blooded animals.

The amount and kind of nourishment.—The amount of nourishment required within a given time stands, as has been observed, in the closest relation to the greater or less func-

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tional activity of the individual organs, to the size of the animal, and also, as I must now add, to its special adaptation to a certain mode of life. It is clear that a large animal must consume actually more food than a small one, but with relation to the mass of the animal the proportion may be precisely inverse. Thus we know that a caterpillar, at the period of its most rapid growth, eats a great deal more in proportion than a dog or an elephant. The determination of the absolute and relative amount of nourishment needed by different kinds of animals is extremely difficult and of no importance to the present enquiry. It offers, indeed, only two points of more general interest, of which one shall at once come under discussion, while the other—the relative amount of nourishment required by carnivorous and herbivorous animals—will be treated later.

The amount of daily nourishment needed differs very widely in individuals of the same species; one will eat, another will drink, more than others; but they will all be apparently equally thriving, excepting in cases of actual over-eating or privation. Between these two extremes—which both result in death, because the maximum of utilised nutrition is exceeded or the minimum is not attained—there is a graduated scale of quantities, which are less and less favourable as they approach these dangerous extremes. Hence a point must exist between the two, which is the most favourable as regards the mass of food introduced into the stomach. This may be briefly designated as the *optimum* of food. But this optimum does not lie, as it might be supposed that it should, exactly halfway between the two extremes, but may lie, according to the creature's needs, nearer to the one or the other. It is, of course, of the highest interest to ascertain what the optimum of daily nourishment is for different animals, since this must be one of the most potent influences which govern the constantly varying numbers of species and individuals. Unfortunately no data of general value exist on this point.[10] We know, with tolerable accuracy, the optimum of nutrition for man, for the domestic animals, and for those that have been subjected to physiological experiment; also for some others, such as many birds and insects, which are of interest to the husbandman. But this

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knowledge, in itself but small, has been acquired either by casual observations or by experiments which relate almost exclusively to such animals as are useful or injurious to man, and the general biological bearing of these proportions has as yet been in no way verified by investigation. Hence I shall avoid giving any specific data, and it will suffice to repeat once more that every deviation from the optimum of nutrition (as to quantity) must be more or less injurious to the creature.

The quality of the nourishment has, if possible, an even greater influence on the life of the individual and consequently on the species, and it constitutes one of the most powerful influences for adjusting the relations between animals and their surrounding circumstances. There is scarcely a constituent of the earth's crust, whether on land or in water—not an animal nor a plant, whether living, dead, or even in decomposition—which does not afford nourishment to some living animal. Some insects live in dried wood, others on living leaves or roots. Almost all the species of Holothuria (sea-cucumbers), many sea hedgehogs, and one genus of Mollusca (*Onchidium*) swallow sand or mud, while neglecting the animals and plants which lie close at hand. Parasites suck the blood of their host or absorb the juices of a particular organ; certain larvæ of Ascaris (*Ascaris nigrovsnosa*, in the frog) consume the organs of their own parent; and human flesh is a tit-bit to some of the human race. But in these, as in all other cases, animals require two quite different kinds of food; it must be of organic and of inorganic origin. If one kind of nutrition is omitted, the other kind, exclusively supplied, will no longer have the same favourable effect on growth and the other vital processes that it had when duly mixed with the other kind. This fact is universally recognised with regard to man and the domestic animals; but it obtains throughout the animal kingdom, though it is not in all cases so plainly apparent. Thus, for instance, Parasites—such as tapeworms, threadworms, &c.—seem to require one kind only of organic food, since they live in certain organs only, one species in the liver, another in the intestines, others again in the brain (as the worm which gives sheep the staggers) or in the eye, the skin, and even in the bones. All these species of

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animals take in only the one form of nourishment which they find in those organs in which they take up their residence; and, in a certain sense, we are no doubt justified in saying that these animals live solely on organic food. But when we remember that the fluids which permeate those organs invariably contain a larger or smaller quantity of salts in solution, this contradiction does not seem, accurately speaking, to exist; for it must evidently be quite immaterial whether an animal takes up the earthy salts and water which are indispensable to its existence directly in their original form, as we do, or indirectly in the juices of the animals or plants on which they feed; only in the latter case, if the amount of inorganic matter contained in the organ is sufficient for its needs, it will require no further addition of salts or of water.

Recent physiology establishes the fact that in man and in the few animals physiologically experimented on, the proportion of inorganic and organic food must always be approximately the same, if health is to be maintained unimpaired. We know moreover that nourishment, at least for man, is taken in combinations in which a conspicuous part is played by stimulants, which by their presence excite the glands in the mouth, stomach, &c., so that they fulfil their office more effectually. The most universally used stimulant is salt. We may very fairly suppose that a similar proportion between organic and inorganic food is necessary to all other animals, and also that they need a mixture of innutritious stimulant with their food; for instance, we know that Ruminants are very fond of salt. But we have no general and verified data on this subject, and the only theory we can assert with any degree of probability is that the stimulants, if any, needed by the lower animals must be quite different from those required by man and the higher animals.

Irrespective of salt, these stimulants—or excitants—consist, for man, principally of wine, beer, and other alcoholic drinks, of coffee, tea, &c., and the various spices. Although we are now speaking of them as in contrast to nutritious food, properly speaking, because they are not transformed or assimilated into living organic tissue, they would seem to be almost indispen-

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sable aids to the assimilation of the true nutriment. They may be compared to the oil needed for the working of every machine; this does not add to the effective power of the machine, whatever that power may be, and yet it cannot work smoothly for any length of time without it. It is in the same way that stimulants enable the body to exert its digestive powers to the utmost. Can other animals dispense with such an 'oiling of the machine'? This gives rise to the question as to what sort of stimulants they need; and to this other one: Whether substances which certainly are by no means stimulants to man may not prove to be such to the lower animals. And finally a third question occurs: Whether other influences, irrespective of the actual reception of food into the intestinal canal, may not act as powerful stimulants for the absorption of true nourishment. This last question may for the present be regarded as superfluous, but it seems advisable to point out that in Chapter VI., 'On the Influence of Stagnant Water on the Creatures inhabiting it,' evidence will be adduced that in certain of the Mollusca (*Limnæa*) the assimilation of nourishment depends not merely on the food itself, on the healthiness of the organs, on the temperature, &c., but also on the influence on the skin of a certain constituent of the water at present unknown to us.

Organs for taking in, preparing, and assimilating the food.—Everyone knows that digestive organs of some kind are possessed by every sort of animal, and it may be taken for granted that the general structure of these organs and their mode of action are generally well known, so that it will be superfluous to describe here the endless variety of such parts; every text-book of zoology gives ample information on such points. A general outline of the relations of the parts must, however, be briefly given. In the first place, their position, invariably within the body, is worthy of remark, since it is this which necessitates the presence of other organs which have certain auxiliary duties to perform in the service of their masters—the stomach and the intestines. The organs for taking up food, the mouth, teeth, and, more remotely, the fore extremities or other external parts, are specially adapted to

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secure food, to divide it, and to transmit it to the stomach after being well comminuted; while man also requires the assistance of the cook in the preparation of his food. Now although, from a physiological point of view, these auxiliary organs are of less importance than the digesting intestinal canal, they are of the highest interest for us, inasmuch as they involve an endlessly varied series of links between animals and the conditions under

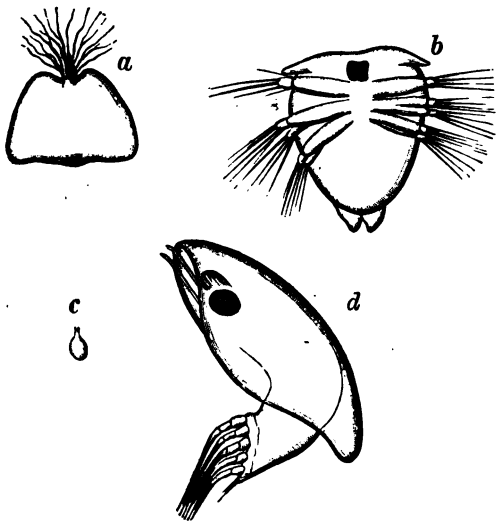

FIG. 12.—*Sacculina carcini*, with the tuft of clinging roots which it inserts into the body of its host; *b*, its larva (Nauplius); *c*, *Thompsonia globosa* (Kossmann); *d*, its larva, Cypris stage.

which they live, in addition to those which arise from the mere quality and quantity of the nourishment required.

The peculiar mode of taking up nourishment exhibited by various Parasites must also be shortly described. As a rule, almost without exception, the larvæ of parasites swim or move freely about in water (leading a very unfitly termed active life). During this stage of free locomotion the larvæ are usually high in the scale of structure. The larva of the parasitical Copepoda or Cirrhipedia (for instance, of a Sacculina, fig. 12) is known

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to zoologists as a Nauplius. This animal has a nervous system, external organs of locomotion of a complicated character, a muscular system of the crustacean type, a well-developed intestinal canal such as is found in the Nauplius larvæ of the lower crabs that are not parasites, and usually even special organs of sense—eyes. Gradually this Nauplius, after attaching itself to the gill or skin of a fish, or under the tail of a crab (Sacculina), loses its organs of locomotion, the greater part of its muscular and nervous system, its organs of sense, nay, often its mouth, stomach, and intestinal canal. Thus the lively crab-like larva is transformed into a shapeless sac, exhibiting no trace by which its crab-like nature can be recognised. Still the creature needs a limb by which to cling to the animal that is to be its host and provide it with nourishment; peculiar clinging organs are developed instead of the lost motory organs (fig. 12, *a*), and these not unfrequently also assume the office of absorbing nutrition from the host. Such, for instance, is the case with the parasitical crabs, which, like Sacculina (fig. 12), live on the abdomen of the hermit crab (*Pagurus*) or of other crabs. They have, without exception, long filamentary processes at the fore-end of the body, with which they cling and bore through the skin of the crab into its abdominal cavity, and then they clasp portions of the crab's internal organs, particularly the liver, in the long entangled filaments. These slender threads are thin-coated tubes which open into the body cavity of the parasite, so that it is highly probable that these clinging threads also serve the purpose of suckers, since they are capable of absorbing nourishment in a fluid form through their thin tissue; at any rate, they do not convey it into an intestinal canal, for the parasite has none. This, however, is no argument against the assumption that the fluid thus absorbed by endosmosis through these roots or suckers serves as food; for we know that in all animals which have a body cavity and dispense with a vascular system the food must first pass into the body cavity, in order to be conveyed from thence to the organs situated on it. So far as regards the part taken by the clinging filaments as organs of nutrition to the parasite, it is perfectly indifferent whether the nutritious fluids to be assimilated first pass through

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the intestine into the body cavity, or, as in Sacculina, are conveyed to it directly by the suckers.

We hereby see that the ways and means by which animals obtain the food they need are very various; even mere external appendages of the body may, like the roots of Sacculina, be transformed into organs of nutrition. But there are other ways in which we see an essential difference in the mode of obtaining nourishment that characterises different animals. All animals that have well-developed internal organs of nutrition are compelled, under the influence and guidance of their will and their subjective sensations of hunger and thirst, to make more or less vigorous voluntary efforts to obtain the amount and kind of nourishment they require. Even animals of such simple structure as the Infusoria obey this law, though their intestine, stomach, and mouth do not constitute separate organs, but only are portions of their protoplasmic body, and though, like all other one-celled animals, they absorb their solid food direct into the digesting protoplasm; still they manifest liking and aversion for different kinds of food, just as much as the higher animals; they never swallow that which they dislike, even when by some accident it comes into contact with their mouth at the same time as the food they prefer.

The case is quite different with all those true Parasites which dispense altogether with a true intestinal canal; they can take up nourishment only in a fluid state, as their skin alone is capable of absorbing it by osmosis, and this is quite independent of the will of the creature. Thus the Cestodea, the curious parasitical snail Entoconcha, several parasitical Crustacea in their fully developed state, the parasitical Trematoda (as the liver Distoma), and even some insects—all of which absorb their nourishment through the skin without having any intestinal canal—depend for their life and wellbeing on the osmotic relations between their skin and the fluids surrounding them. Now, as osmosis through the skin—*i.e.* the absorption of the fluid nutriment in the surrounding medium—can never, so far as we know, be interrupted, all these animals are compelled to be incessantly taking up and assimilating food. Thus the parasite is quite incapacitated from making any choice in the

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nutriment supplied to it, since it is fixed in the skin or in some particular organ; and moreover it must always perish if by any circumstance the fluids which bathe its skin are so far altered as to cease to be fit to nourish it.

From these circumstances it will be at once understood that there is a fundamental difference between true nutritive matters and certain other substances. If indeed, as is sometimes done, we choose to call everything food which may be in any way concerned in digestion and the absorption of the gastric juice or a partial conversion into organic substances, heat, and motion—irrespective of how or through what means the matters were conveyed into the organism, and so rendered efficient—we shall be forced to apply the term not merely to oxygen and ozone, which are taken into the body by respiration, or water and salts, which are introduced in the most various modes—often through the skin—but to all the other influences which are indispensable to the life and growth of every individual. Nay, even the sunbeams with their waves of heat and chemical light must be included, for without their aid the stomach and intestines could not fulfil their functions, any more than the gills or lungs, the brain or the organs of sense could carry on theirs without healthy nutrition through the intestine. Hence we are justified, while investigating the effects of nutrition on the animal organism, in directing our attention solely to those internal organs of digestion which demand the collaboration of external auxiliaries, and in leaving absorption by the skin quite out of the question; for although this process, as regards its effect on the life of the individual, acts precisely like the true nutritive function, it induces no other connection with the external conditions of existence than those which subsist in all animals through the skin and its relations to the medium surrounding it, whether air or water, &c. These relations never demand any special auxiliaries that depend on will, inclination, or disinclination, since the efficient action of the skin, in all such cases, depends merely on the molecular relations between it and the fluid matter with which it is in contact.[11]

The results we have so far arrived at may be thus shortly recapitulated. We have seen that food, in the strict sense,

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gives rise to various relations between the animals and their surroundings in the following manner. All animals need a certain optimum of food; being compelled to take organic as well as inorganic food, they are dependent on plants, which alone are able to form organic compounds by the decomposition of carbonic acid; both the quality and quantity of the food lead to a vast number of very various relations between the animals and inorganic nature on one hand, and living beings on the other; finally, the organs which are auxiliary to the acquisition of food are in direct connection with the animal's mode of life.

Every modification of these relations once established must necessarily exercise an influence on the animals in contact with it, and in this case, as in all others, this influence may be twofold: selective or transforming. The great variety, as has been briefly indicated, of these conditions and relations requires us to discuss a few cases of more conspicuous interest, in order to understand how far food does in fact exert a direct or indirect influence on different animal forms.

Monophagous and polyphagous animals.—Any division of animals into two such groups as are here indicated has obviously none but a purely physiological value, nor is it a thoroughly comprehensive one, as we shall immediately see; although a very conspicuous contrast exists, and has a certain value, between Monophagous animals—consuming, that is to say, only one kind of food—and Polyphagous creatures, which eat a variety of food or even anything that comes in their way.

If we confine our attention to the distinction between the two kinds of food, vegetable and animal, we may regard all purely carnivorous or purely herbivorous animals as monophagous; but within each of these groups there are animals that are monophagous in the strictest sense of the word, several species being fitted in fact to feed on one kind only of organic food. A closer enquiry into the conditions resulting from this will be of interest.

In the first place, it is clear that a certain interdependence between flesh- and plant-eating animals must exist, and find its expression in the proportional numbers of individuals of

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the two groups generally distributed over the face of the earth. We know that its surface—dry land as well as land covered with water—is capable of producing only a certain limited number of plants, depending on the conditions of the locality. Assuming then that a given number of plants—the maximum number being present at the time—offered, let us say, a thousand units of food to these two classes of animals, the carnivorous and herbivorous species would not be able to have an equal share of the space and of the food it would afford. The flesh-eaters would only obtain food from the soil indirectly through the plant-eaters. Now the transmutation of the nutriment derived from the plants into the flesh of the plant-eaters is inseparable from a certain loss in the whole mass, since the oxidation of a certain amount of the organic constituents is necessary for the production of animal heat and for the movement and due use of all the functions of the body. Now we will assume—quite arbitrarily—that the proportion of the whole mass of plants produced by the soil is to the animals which can subsist on them—converting them into animal tissue—as ten to one; then, in the area we have assumed, only 100 units of feeders—individual Herbivorous animals—can live on 1,000 units of plant food. The maximum of nourishment, then, which exists for monophagous carnivorous animals, can amount only to 100 units. In the transmutation of these 100 units of food in the organs of the Carnivora a considerable loss will be incurred; organic matter will be consumed, the indigestible portions, as hairs, hoofs, and horns, will be ejected, and if the proportions were such that ten units of animal food could suffice only for one unit of the animal body, the maximum of food as supplied by 100 herbivorous animals would enable 10 carnivora at most to exist. Thus the same area can never produce and maintain so large a number of carnivorous as of herbivorous animals, an inference which is perfectly confirmed by the facts. It is well known that the number of Herbivora is much greater than that of Carnivora; and in connection with this fact is this other, that among the Vertebrata, those at any rate that commonly live in large herds, are vegetable feeders, while the individual Carnivora, which are on the whole much less numerous,

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display a much greater disposition to separate themselves into small families. Thus the number of individuals of the monophagous animals depends in a great degree on the nature of their food; and even the most primitive habit of life, *i.e.* the instinct of living apart from their fellows, or of living associated in large herds, is very decidedly influenced by it, if not actually produced by it.

The dependence of the Carnivora on the Herbivora thus clearly indicated, leads to another question—that, namely, as to the possibility of animal life existing where no plants can grow, and where consequently no vegetable feeders can live. We know now that, contrary to the opinion which for a time prevailed that the bottom of the sea was uninhabitable, a considerable number of the most various creatures live in spots where the sun's rays never penetrate, and where, therefore, no plant can grow. According to Forel, plants containing chlorophyll cease to be found in the Lake of Geneva at about one hundred fathoms, and the limit in the sea seems to be about the same. Nevertheless, in the Lake of Geneva, which is much more than one hundred fathoms deep, and everywhere on the floor of the deepest Atlantic, we find a multitude of living animals. These, at such great depths, cannot feed on living plants; they must all be flesh-eaters, as has been confirmed by observation. But as they cannot form organic matter from carbonic acid, water, and ammonia, they must soon infallibly perish if no substitute were provided for the animals destroyed for food. Hence we may be allowed to assume that the organic food found in the plants at the surface of the sea is in some way conveyed to some of them. Professor Möbius of Kiel has lately undertaken the investigation of this problem. He came to the conclusion that the organic matter produced at the surface of the sea by the decomposition of plants and animals is carried down to the bottom by the Sinking Current, as it is called, which results from the difference of temperature at the bottom and at the surface; this theory, however, cannot be regarded as proved by the experiment which Möbius made for that purpose. In small aquaria which were perfectly protected from any shock, variation in temperature produced sinking currents,

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which sufficed to level gradually, but completely, the uneven mud at the bottom of the aquarium. Now it is true that we know that many currents occur in the ocean which reach to the bottom, and which, as they take their rise at the surface in remote localities, seem specially adapted to convey food from above to the deep-sea creatures. But Möbius himself points out that one assumption is still unproved by this—namely, that the organic portions of the plants and animals that fall from the surface must remain undecomposed in their journey if they are actually to serve as food for the animals there. Whether this is the case we do not know, and this really ingenious theory remains for the present unproved, and may perhaps be ere long replaced by another not less plausible.

We will now enquire more closely into a few striking phenomena connected with the monophagous habits of certain animals, and endeavour to demonstrate, by the discussion of a few examples, the extremely diverse conditions which appear to be produced by the adaptation of various animals to one single kind of food. It is clear that an animal to whose existence one particular sort of food is indispensable must be the slave of that plant or animal which alone can supply it; such a monophagous creature must consequently, in many cases, be adapted to the same mode of life as the organism on which it lives. Many birds live, as is well known, exclusively on hard seeds. Now, as the beak of a bird is but rarely adapted to crush such seeds or grains, the grain-eating birds must possess another organ with which to reduce them. This organ is what is known as the gizzard. This has on its inner side a very thick, hard, brown skin, which is admirably suited to triturate the hard grains by the aid of the grains of sand and small pebbles which are swallowed at the same time, and to protect the softer portions of the stomach against the ill effects of the sand and stones. Thus we here find a peculiarity which enables its possessor to avail itself of a particular supply of food, which the birds of prey with their soft stomachs are unable to take advantage of. A still more striking illustration of the fact that such organs, calculated for a single kind of food, sometimes appear under very unexpected aspects, such as by all school theories would be

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considered impossible, is afforded by the genus *Dasypeltis* among the snakes; the species occur in Africa and live on birds' eggs. They swallow their food—the eggs—as other snakes swallow frogs and fishes, snails or mammals. But the nourishment contained in the egg is enclosed in a calcareous envelope—the egg-shell; if the snake, in order to get at the contents of the egg, were able to crush it by its teeth and jaws, it would certainly lose the greater part of the fluid contents. The only way to lose nothing of it, therefore, is to swallow the egg whole; and in point of fact it does reach the stomach un-

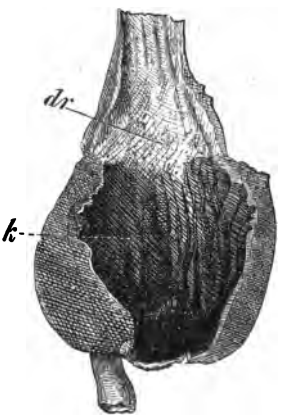

FIG. 13.—Section of the œsophagus and stomach of the Pigeon. *dr*, the glands; *k*, the gizzard, enclosed in a thick brown skin.

broken. But here organs have developed in a most marvellous way, which, in all other cases without exception, are confined to the bones of the mouth, namely, teeth. These occur firmly set on the lower side of the vertebræ and in the forepart of the stomach, and their points pierce through the coat of the stomach so far that they seem to be purposely fitted for breaking the eggs passing through it; in fact they must work in this way, for they are the only part of the stomach strong enough to be able to answer this purpose. This is, as has been said, the only instance of true teeth, acting as such, occurring in any other situation than on the bones which surround the cavity of

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the mouth; but it is an exception which, as we see, is due to the propensity of the species of *Dasypeltis* to make the eggs of birds their exclusive food.

These few examples, to which others could easily be added, for many are universally known, will here suffice to prove that monophagy in animals is often connected with the occurrence of special organs or relations of structure, and that the preservation of such species is solely due to their efficiency. Their inefficient development would infallibly lead to the destruction of the species—taking it for granted, of course, that it was unable to accustom itself to any other food.

Sometimes adaptation to a single kind of nourishment does not depend, as in the cases here considered, on the existence of a special organ, but on a peculiar cycle of development in each individual animal. This, for instance, is the case with all the Intestinal Worms. These must become extinct if their larvæ were not able, or even forced, to migrate and to seek food in other spots away from their parents. If we suppose that the Tapeworm, or even the Trichina, were capable of going through the whole cycle of its development within the same host, its permanence as a species would be possible only if all men were habitually cannibals. Corresponding to this we find that all Intestinal Worms have to go through a longer or shorter period of migratory existence as young and sexless creatures or as larvæ. They at the same time change their host several times—for they often become parasites from the first, after a short period of free life in the water—till at length they are sexually mature, and have found their way into an animal or an organ similar to that which they left in the embryo or larva state. All internal parasites are subject to this inevitable law of migration—such, that is to say, as live in the interior of an animal structure or of its organs. It is applicable even to the well-known *Trichina spiralis*, which is capable of going through all the stages of its development in the same animal, but which nevertheless travels, in its youth, from the intestine outwards to the muscles. From them, however, it is incapable of returning to the same intestine, although it would be perfectly capable of achieving sexual development there and of producing eggs; it

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must absolutely pass out from the muscles to the intestine of some other creature—a rat, a mouse, &c.—in order to pass, in the second generation, back again into the human intestine. If the Trichina from the muscle does not pass again into the intestine of some other creature—which is, of course, commonly the case as regards human beings—it infallibly dies, although its tenacity of life is enormous; such a Trichina can live for ten years enclosed in a muscle. Here the permanence of the species, as such, depends on the capability of the larvæ for migration, and for finding their nutriment in other animals which may secure their transfer into those in which alone they can find the special food that is necessary for their full development, and for the exercise of their sexual functions. If a young parasite were to lose its way, or to be swallowed by an unsuitable host—a Trichina, for instance, by a Fish—it would infallibly perish unless it were able to accustom itself quickly to the food which is unsuited to it. No such cases, however, are known of adaptation of parasitical worms, when sexually mature, to an unwonted form of nutriment. Thus it would appear as if in these cases, without exception, the change of food involved in the migration of the young animal were of the same service to the species as are special organs contrived for special nutrition in others; the preservation of the species in the former class depends on change of food and migration just as much as, in the latter, it depends on the adaptation and functional activity of individual organs.

A similar dependence of the species on its food does not of course exist among the truly Polyphagous Animals. Their polyphagous habits allow of their changing their food at pleasure without suffering in any way, or at any rate seriously, when, from any external cause, they are obliged to alter their mode of life. It must not however be forgotten that even these animals depend to a certain, if not to a very great degree, on the nature of their food. It is now universally admitted that in many animals a definite relation must subsist between the amount and kind of food if the animal is to derive the greatest possible advantage from the food consumed. Man in this respect offers the best known instance. Starchy food or sugar,

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fat or meat, salt, water, and stimulants must be obtainable in certain proportions—which may be designated as the optimum of nutrition—if they are actually to produce all the effects proper to themselves and beneficial to the human organism.

We are certainly justified in supposing that similar relations exist between the various constituents of the food of the other polyphagous animals. But we know nothing or very little on this subject, although it would be very interesting to learn whether similar relations in the admixture of these constituents subsist for the lower animals as for man; or, on the other hand, quite different ones—for low forms of polyphagous animals, for instance, as Insects, Crustaceans, and Molluscs. At present, therefore, an enumeration of polyphagous animals has no interest, since we cannot learn from it anything as to the dependence of the polyphagous animals on any definite mixture of food, or as to their absolute independence of it.

Many cases of polyphagy are of the highest interest as considered from another point of view. In connecting and comparing the physiological activity of an animal with its position in the general system, we might perhaps expect to find that all the species of a genus, and still more all the individuals of a species, would be equally dependent on the same mixture of food; and we should be particularly inclined to this assumption in all those cases in which, as we know, the consumption of food directly depends on the presence of one particular organ of definite structure and action. Such a conclusion would nevertheless be wholly unjustified. We will for the present postpone the question as to how far different individuals of the same species may be capable of varying their nutrition, and will here only investigate those cases which show that many polyphagous species are found in genera which otherwise contain none but monophagous Carnivora or Herbivora.

The greater number of Parrots are, as is well known, vegetable feeders—live, that is to say, on grains and fruits. Many, however, eat insects eagerly, and even meat; and it seems to be a tolerably general custom in zoological gardens to add a certain proportion of fat to the vegetable food of the larger parrots. The Lizards of the Eastern hemisphere are, almost with-

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out exception, carnivorous; those of the Western, on the contrary, chiefly herbivorous. But among the former there are certain species—*Lacerta agilis*, *L. muralis*, and others—which sometimes, like dogs, eat grass and even fruits. On the Balearic Island of Ayre, close to Majorca and Minorca, lives an entirely blue-black variety of *L. muralis*, which I myself found there. The island is very barren; only low shrubs grow on the stony soil, and during the dry months, from June till October, not even burrowing insects are to be found. During this period the lizards feed on plants, and above all on the fruit which is brought in by the inhabitants. I have been able to keep numerous specimens which I brought away with me, for months together, even during our northern winter, on sweet fruits, juicy or softened by soaking. Now in all text-books of zoology it is stated that the lizards of the Old World are distinguished by having teeth connate with the jaw, while the vegetable-eating lizards of the West have teeth which grow in sockets in the jaw. The facts above given suffice to show that this parallel between the nutrition and the animal's place in a system—such as seems to be indicated by the teeth—is in fact defective in individual cases, and we may even hazard a suspicion that it may in great part depend only on insufficient observations of the habits of lizards on the part of zoologists. Most small apes feed on fruits; amongst them, however, *Jachus vulgaris*, known as the Marmoset, is distinguished by an inordinate liking for the ill-smelling cockroach, a species of *Blatta*. Our common perch, as well as a few Cyprinoidæ, frequently eat duck-weed (Lemna), although they belong to a group of carnivorous fishes; squirrels are the greatest enemies of our singing birds, whose eggs and young they devour in great quantities; individuals of the Russian brown bear will feed on oats, others on honey, others again on ants or meat. In conclusion I will only mention one fact frequently observed in aquaria by myself and by others. The well-known European pond-snail, *Limnæa stagnalis*, belongs to a group of Mollusca which all live on vegetable matter; and their lingual teeth are regarded by malacologists as typical of true plant-eaters. Nevertheless, the Limnæa is fond of eating the little water salamander, Triton. I have often observed them sud-

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denly attack quite healthy living specimens of *Triton tæniatus*, overcome them and devour them, although the aquarium was full of luxuriantly growing plants, on which these water-snails usually feed.

These instances[12] will, I think, suffice to warn us to be cautious when, from the systematic position of an animal and the structure of its organs, we are called upon to determine what may be its mode of life and nutrition; they further teach us that a polyphagous animal can occasionally be easily trans-

FIG. 14.—*Larus argentatus*, one of the species of gull experimented on by John Hunter.

formed into a monophagous one without suffering any serious injury.

Thus, in general, polyphagous animals are less dependent on their food than monophagous species, and hence food can exert only a weaker selective influence on the former than on the latter. Assuming, for instance, that there were an animal which, up to the present time, had been fitted to use a certain species of animal or plant as food, and that it were suddenly transferred to a foreign country where such food was lacking, or that the animal or plant serving it for food were extirpated, while the creature itself was not; in either of these cases the continuance

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of the species as such might be made possible if the surviving specimens could quickly accustom themselves to the effects of a change of food. Such an accommodation to a new diet, not properly suitable to the animal, might be expected to be almost impossible to monophagous creatures, but to the polyphagous far less so.

However, many animals of both groups are already known which are able, intentionally or under compulsion, to change their food, and in a corresponding degree their mode of life. The well-known anatomist and physiologist, John Hunter, long

FIG. 15.—*Myopotamus Coypu.*

since communicated his observation that a kind of gull, *Larus tridactylus*—can live on grain, although its stomach is adapted to flesh diet; it commonly feeds on fish. Another species, *Larus argentatus*, is said by Dr. Edmonstone to live in the Shetland Islands on grain in the summer, and on fish in winter. In the same way the Coypu—*Myopotamus Coipu*—living in the Chonos Islands, off the western coast of South America, has accommodated itself to an animal diet; it there chiefly eats the marine mollusca of the coast, where alone the creature is found; on the mainland, high up the country, it feeds exclusively on roots, which it digs out on the shores of streams and

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brooks. A very interesting example is offered by the Kia—*Nestor mirabilis*—of New Zealand; it is allied to the parrots, and formerly fed on the juices of plants and flowers, but lately it has become accustomed to sipping the blood of newly slaughtered sheep; and it is asserted that this bird, originally so harmless has actually become a serious foe to the flocks of New Zealand by its constantly increasing love for the blood of sheep, for it even pecks and sips the most minute wounds on a living sheep, and so sets up an irritation which not unfrequently leads to the death of the animal. Dr. Philippi, the best known

FIG. 16.—*Nestor mirabilis*, a New Zealand parrot.

zoologist of the University of Santiago in Chili, has recently communicated a still more remarkable case. Two horses on the estate of a certain Mr. Nicholas Paulsen, according to him, had for weeks indulged in the bad habit of eating every day some of the young pigeons and chickens in the poultry-yard.

In the Zoological Institute of Würzburg, I have kept for six years a pair of fully grown and perfectly tame prairie dogs. The male, to which I gave the old-fashioned German name of Hans, differs entirely in his tastes from the female, Gretel. She, in every respect an ornament to her sex, always gentle, unassuming, and affectionate, but very timid too, prefers a vegetable diet—fresh

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plants, bread, nuts, corn, &c.—although she sometimes does not disdain meat and liver. Hans, on the contrary, bold, eager, and suspicious, a true tyrant withal over his wife, is passionately fond of everything he can get in the way of animal food. Formerly, when aquaria stood in the room in which Hans and Gretel lived, he often tried to catch fish or crustaceans, which he devoured eagerly; fat, liver or meat, eggs or frogs, ant's eggs or insects—in short, every kind of animal food—is acceptable to him, and he laps the blood of freshly slain beasts with the utmost satisfaction. It is evident that Hans first became accustomed in my laboratory to most of these articles of diet. In itself the matter certainly is not so very surprising, since most—or very many—rodents are polyphagous, or even omnivorous animals; but it is rendered interesting by the fact that the female has by no means accustomed herself to an animal diet in the same way as the male.

This brings me to an observation which, in the course of my travels, I once had occasion to make very much against my will. The Egyptian crocodile — *Crocodilus biporcatus* — is, as we know, very widely distributed, and it lives in great numbers in the rivers and on the sea-shore of the Philippine Islands. In Egypt this creature is considered extremely dangerous, and is said to have a particular predilection for human flesh. When I was travelling in the Philippine Islands I was often told by the natives that they distinguished two sorts of crocodiles, of which one ate men in preference to other food, while the other did not; several of the former were said to be well known to the natives, and in Cagayan in Luzon, where I saw the skeleton—quite 22 feet long—of a crocodile caught not long before, I was assured that a gigantic anthropophagous crocodile lived in the river and could not be caught, and had for years been known to the natives by a particular nickname. I was much inclined to doubt this story till I went through a little adventure which made it seem to me certainly by no means improbable. On one of my excursions in the north-east of Luzon we (my servant Antonio and I) had crossed a wide but shallow river early in the morning in a canoe; when we returned in the evening the canoe had disappeared, and not a living soul was to be seen anywhere. After long waiting in vain we decided on walking

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through the stream. I, in order to preserve my watch and other instruments from a wetting, seated myself astride on Antonio's shoulders. When we were about halfway across, where the water reached nearly to my bearer's neck, a man appeared on the shore. Seeing him I shouted out, half in jest, 'Are there any crocodiles in the river here?' My feelings may be imagined when I received the answer, 'Oh, yes; there are plenty of crocodiles in the water, but they will not eat men.' Everyone will be reminded by this story of the many similar ones of sharks, alligators, and other animals, which all concur in proving that these creatures exhibit the most remarkable preferences in the choice of their food, and that even individuals of the same species differ widely.

It will be unnecessary to adduce any further examples or even to investigate the credibility of these current stories regarding crocodiles; for, even without these, the instances given above suffice to show that polyphagous or monophagous habits are not immutable characters, but that, on the contrary, almost every species is able more or less to vary the nature of its food. Hence the dependence of an animal on its nutrition is not absolute, and consequently the selective influence of the nutrition is, as we see, in some degree limited by the animal's capability for accommodating itself, with very various results, to a diet hitherto unknown to it. The selective influence must, at any rate, remain tolerably great, particularly on monophagous creatures; and it is more than probable that a sudden and rapid change of nutrition, such as may sometimes be forced upon animals by external circumstances, will inevitably lead to the equally rapid death of most species.[13]

Now, if we suppose that such a sudden change of nutrition actually were imperative on several species at once—such, for instance, as always occurs in the migration of many marine creatures, and of all parasites—some species must perish, because they would not be capable of living on the unaccustomed food; others might survive because they were omnivorous or because, even though monophagous, they were able to adapt their functions promptly to the new conditions of life. In the latter

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case the structure of the animal and of its organs might remain unaltered in spite of the alteration in the nutrition, as, for instance, seems to have been the case with the Coypu, those of the Chonos islands not differing in any way, so far as we know, from their congeners on the mainland. But, finally, this change in the food might have altered the structure of some organs, particularly of those most directly interested, so far as to make these changes conspicuous; and a direct modifying influence exercised by the conditions of existence afforded by the food would be thereby proved.

The direct modifying influence of food.—It is universally known, and has never been denied, that the amount of food exerts a very decided influence in determining the growth of the individual and of its organs, as well as on its whole size; but this has often been tendered as a means of explanation in certain cases which have not been submitted to careful investigation. It can never, of course, be disputed that an animal must take up the optimum of daily nutrition, which constantly varies with its advancing age, in order to attain its normal size; we might even declare our opinion that very many living or extinct animals might have grown to a size far beyond that which they have in fact attained, if they had had more abundant supplies of food at their disposal; but it would be in the highest degree illogical to assume, on the contrary, without any experimental proof—as is unfortunately almost universally done—that the small size of any particular animal in any particular locality is invariably induced by a deficiency in the food attainable there, where the optimum is seldom or never attained. In these cases, as in all others, in consequence of the extreme complication of the animal body and of its functions, the same effect may be produced in many different ways.

But the amount of food attainable affects not merely the size of the animal, but also determines, and even modifies, certain vital functions. It is self-evident that an optimum of nutrition can alone insure the normal functions of all the organs; if it does not attain the optimum, the functional activity of all the organs is impaired; modifications at the same time occur in their structure, *i.e.* the animals grow leaner, become

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incapable of exercising their sexual functions, &c. In this respect the most interesting examples are those of the influence of deficient nutrition on the larva forms or on the conditions of development. Unfortunately next to nothing reliable is known on this subject, and it is much to be wished that the various observations that have been accidentally made and interpreted 'to taste' should be made the starting-point for actual experimental investigations on this question. I will here mention a few of what seem to be the most trustworthy of these. Mr. T. Gentry, of Philadelphia, has shown that the larvæ of a moth —*Acronycta* sp.—entirely lose the habit of spinning a cocoon before assuming the pupa state when their food is insufficient, and that both the pupæ and moths are then smaller. The observations independently made on the Hydroid Polyps by Hincks, Allman, and Schneider are highly interesting. According to these, in the first place a Medusa of the group of the Hydroida can be induced by lack of nourishment to assume the polyp-form, *i.e.* the larva form of the species. Secondly, the hydroids of the higher Discoid Medusæ—as *Medusa chrysaora* and others—produce much fewer Medusæ in confinement than in the open sea; and this has been accounted for, somewhat hastily, by the assumption that deficiency of food is the cause. Experimental proof of the accuracy of this hypothesis has not, however, been adduced.

The **quality** of the food, next to the quantity, exerts a direct modifying influence which in many cases exhibits itself in the organs most nearly interested—those, namely, of digestion—though others may become subject to it. More rarely the whole size attained by the animal may be conspicuously affected by it. But we possess only a few trustworthy observations on this point, interesting as it is, and still fewer available physiological experiments, though such are indispensable. The lack of materials on this subject renders it necessary to discuss it briefly here.

In the first instance the statements of Wallace and others as to the influence of food on coloration must be mentioned, since Seidlitz in his various works attributes great importance to them, although, as it seems to me, he assumes something to be

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proved which, fundamentally considered, is not so. Wallace, for instance, relates that a Brazilian parrot—*Chrysotis festiva*—can be made to change the green in its feathers to yellow or red if it is fed on the fat of certain fishes allied to the shad—a method largely adopted by the Indians. The same traveller further asserts that the splendid Indian bird, Lori Rajah, is said to preserve its gorgeous colouring by a peculiar mode of feeding. The bullfinch is said to turn black when fed on hemp-seeds; recently a splendid orange-coloured variety of the canary has been introduced into commerce, and it is said it is produced by feeding ordinary specimens of the bird on Spanish pepper. The statement is well known that butterflies, and more particularly species of the genus *Euprepia*, assume an abnormal colouring when the caterpillars are fed on leaves which they are not accustomed to; thus *Euprepia caja* becomes quite brown when the larvæ are fed entirely on walnut-leaves. This assertion, however, has been frequently contradicted, and no systematic and experimental investigations, as directed expressly to this end, have ever been made to my knowledge, for the independent experiments in feeding made accidentally or by a happy chance by different entomologists cannot in fact be regarded as physiological experiments. Still less can the statements made by travellers, as by Wallace, count as such, since they rest entirely on hearsay from wild Indians, and not on the results of their own investigations. Of course I am far from asserting that no such direct modifying influence of food on the colour of animals exists, or that it is improbable; I only would point out that up to the present time we know nothing exact on this point, and that nothing is actually proved beyond the possibility or probability of such an influence affecting the skin-pigment of various animals. As to the nature of this chemico-physiological process, which is what is truly worth knowing in the matter, so far as I know, not even a hypothetical view has as yet been expressed.

A few experiments are better established which prove that certain structural relations may be entirely changed by the direct influence of food. The English anatomist Hunter purposely fed a sea-gull—*Larus tridactylus*—for a whole year on

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grain, and he thus succeeded in so completely hardening the inner coat of the bird's stomach, which is naturally soft and adapted to a fish diet, that in appearance and structure it precisely resembled the hard horny skin of the gizzard of a pigeon. Dr. Edmonstone assures us that this experiment is annually repeated by nature; that the herring-gull—*Larus tridactylus*—of the Shetland Islands twice every year changes the structure of its stomach, according to its food, which consists during the summer of grain, and during the winter of fish. This gull then has, in fact, during the summer the stomach of a grain-eater, and during the winter that of a carnivorous bird of prey. The same naturalist observed a similar transformation in the structure of the stomach in the raven, and Ménétriès makes a similar statement with regard to an owl—*Strix grallaria*.

These experiments suffice to prove that the stomach of a carnivorous bird (an owl, a gull, and a raven) can be transformed to that of a grain-eater if supplied for a sufficiently long period with the food requisite for this result. The question then obviously suggests itself whether the converse is equally true, *i.e.*, whether the gizzard of a true grain-eating bird can be transformed into the soft-skinned stomach of a carnivorous bird. The experiments of Dr. Holmgrén in fact prove that in pigeons which are fed on meat for a sufficiently long period, the gizzard is gradually transformed into a carnivorous stomach.[14]

I have not been able to collect a larger number of really credible or experimentally proved data, and I believe that I cannot have overlooked many really important and available communications. I except, of course, the cases briefly given in Note 15 of the influence of nutrition on sexual maturity and on the secondary sexual characters of domestic animals, since we are not justified in directly applying the results derived from the artificially bred races of domestic animals to all others living wild. Meagre as is the list here given, it amply suffices to prove that changes in nutrition are able to exert even a direct influence on many structural relations of organs, although it must be admitted that we know nothing—absolutely nothing—of the limits of the variations called forth by this direct influence

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of a certain diet. The variations in the structure of the stomach of birds experimentally proved by Hunter, Edmonstone, and Holmgrén, have only a superficial importance, since we do not know whether modifications of other parts were connected with them or might subsequently have originated from them. If now we reflect that, in spite of the great general interest of the experiments of Hunter and Holmgrén, not the smallest additional fact has been established experimentally since their time either by modern zoology or, on the other hand, by organic physiology—no one having investigated the subject—it may be regarded as a not improbable opinion that experiments purposely carried out on a large number of animals, as widely different as possible, would offer a much greater mass of results than are at present at our disposal. Moreover, it is not impossible that change of food may lead to more fundamental modifications in other animals than those in the stomachs of the pigeon and herring-gull, since we know that different species react in very various ways under identical influences. The above-mentioned cases of the variations in external colouring produced by food in birds and butterflies sufficiently prove this; for there is a large number of animals in which a change of food has no influence whatever on the skin-pigment.

The conclusion of the investigation conducted in this chapter is not very satisfactory: we have seen that with respect to the direct modifying effects of food everything in fact remains to be done. However, the few well-ascertained cases suffice to prove that the smallness of our stock of positive knowledge on the subject is probably due only to the fact that no systematically pursued investigations have been carried out.[15] This may, it is true, be excused on the score that zoologists—on whom this task would principally devolve, owing to the position taken up by physiologists—have been prevented fulfilling it partly by the direction which the development of their science has taken, but above all by the absolute insufficiency of their institutes and laboratories.

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CHAPTER III.

THE INFLUENCE OF LIGHT.

It has been poetically said that the plants and trees of our time are the incorporate sunbeams of to-day, and that coal contains the sunshine of long past epochs, divided from the present by millions of years; and the saying is to a great extent true, as everyone knows, for the greater proportion of vegetable organisms depend entirely for life and growth on the direct influence of light. It is equally well known that animals are to a certain extent independent of this influence. At the same time even they are open to it, and the question might even be suggested: Whether animals are not in fact at least as dependent as plants on the direct influence of light, even though the nature of their relations may be altogether different? In discussing this point we will distinguish between the heat-giving rays and the light-giving rays, even when these are in the most intimate combination; and we are justified in doing this, since we know that these two modes of motion act upon living organisms in different and often antagonistic ways.

The difference between animals and plants.—If we except the lowest organisms, the relations between light and the organism seem to be maintained by two very dissimilar organic structures—by the eye in the animal, and by the chlorophyll bodies in plants. These, nevertheless, have been occasionally compared.[16] Each organ would seem to preclude the other. It is true we know of some highly organised animals that have no eyes, and true plants which are devoid of chlorophyll; but plants never have eyes at all, and such animals contain no

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chlorophyll; thus in these exceptional cases the influence of light appears to be almost or entirely excluded. We venture to assert that this contrast holds good in by far the larger number of animals and plants, and it is quite certain that true eyes are never found in plants, while it still remains doubtful whether chlorophyll does actually occur, as has often been asserted, even in the lowest animals. Theoretically its existence in animals is certainly not impossible; and this theoretical possibility has perhaps given rise to the assertion. The wide interest which attaches to this assumption may justify us in digressing here into a somewhat closer discussion of the data relating to the matter.

The chlorophyll bodies of plants are, as is well known, microscopic and elementary bodies of peculiar structure and of definite function; their principal property is that they decompose carbonic acid under the influence of light, and form organic compounds by the combination of three or four elements. This true chlorophyll has, besides, properties which allow the botanist to distinguish, when necessary, whether the green colour of a newly discovered plant is actually caused by the presence of chlorophyll, without any need of previously investigating whether the green particles decompose and assimilate carbonic acid. Among these properties are certain absorption-bands in the spectrum of solutions of chlorophyll, its direct dependence on the presence or absence of light, its reaction under certain chemical agents, and its peculiar microscopic structure. In most cases it is sufficient for the botanist to have detected any one of these features when the case in point is to prove whether the green colour of a plant depends on chlorophyll. Besides this, so far as I know, no exception worth mentioning has hitherto been admitted to the rule, that the green colour of all plants is occasioned not by any true pigment, but by the presence of chlorophyll. In animals, however, the case is quite different. We know that most animals are absolutely incapable of decomposing carbonic acid; but they are, nevertheless, frequently of a green colour. In by far the greater number of cases this green colour is undoubtedly due not to chlorophyll, but to a true pigment. Hence we cannot

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without further proof assert the presence of chlorophyll in any animal, even if we could prove the animal's direct dependence on light, or the similarity of the spectrum of the solution of the green pigment with that of chlorophyll, or even a possible agreement in the microscopic structure. Positive proof of its existence can be derived only by evidence of the presence of all the characteristic properties of true chlorophyll in the green colouring matter of the animal. And it may at once be said that the decomposition of carbonic acid by green-coloured animals has never been proved by exact experiment.*

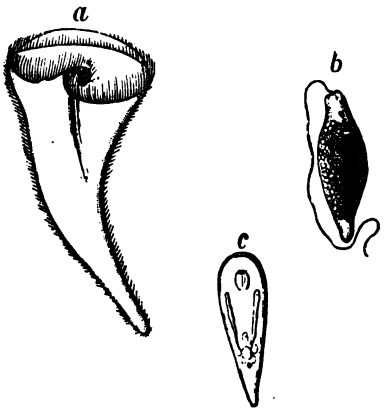

FIG. 17.—Animals in which chlorophyll grains have been detected. *a*, *Stentor viridis*; *b*, *Euglena viridis*; *c*, *Vortex viridis*. The first two are Infusoria, the last is a Turbellarian.

The animals (fig. 17) in which it has been asserted that chlorophyll is present, belong exclusively to the Invertebrata. Among the Protozoa the following are the best known; Euglena, Stentor, many Radiolaria and Spongilla; the green fresh-water polyp Hydra among the Cœlenterata, and a few Turbellaria among the worms.[17]

The arguments for the statement that the green colour of these creatures is actually due to chlorophyll are many and

* Such a decomposition has been recently proved by the experiments of Mr. Patrick Geddes on the green Turbellarian worm, *Convoluta Schultzii*.—(TRANS.)

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various. Mr. Sorby has shown that the green variety, or species, of our common fresh-water sponge (*Spongilla fluviatilis*) owes its colour to minute particles of colouring matter which seemed to be identical with chlorophyll, for he proved that their spectra were identical. The same method was followed by Mr. Ray Lankester, who, with regard to Spongilla, came, it is true, to a conclusion different from that of Mr. Sorby, but, on the other hand, recognised the presence of chlorophyll in *Hydra viridis*. The much-lamented Max Sigismund Schultze, to whom we owe the earliest accurate observations on animal chlorophyll, endeavoured to prove its identity with vegetable chlorophyll by comparing the chemical reactions of various solutions of each, as well as by observing that *Vortex viridis* loses its colour in the dark, and that the animal, exactly like plants, always seeks the lightest side of the aquarium. But the decomposition of carbonic acid by animal chlorophyll has never been demonstrated, although Sorby himself has pointed out that it would be very interesting to know whether such a process does actually take place in animals that contain chlorophyll; for if the decomposition of carbonic acid could be ascertained in these low forms of animals it would prove that they are able to elaborate and assimilate inorganic matters in the same way as plants, though they also, like all other animals, require ready elaborated organic nourishment, or they cannot thrive But this would be a fact of very far-reaching significance, exhibiting a certain affinity to the instances known to us of carnivorous or insect-eating plants (Drosera, Dionæa, and others).

At the same time it must be pointed out, on the other hand, that—granting unconditionally that the pigment of the animals that appear to contain chlorophyll is truly of the nature of chlorophyll—its presence in animals may be explained in two different ways. In the first place, if the chlorophyll bodies of a *Stentor*, for instance, were really elements of the animal tissue, elaborated from its protoplasm by the direct influence of light, then—but only then—might we say that there were actually animals which assimilate in the same way as plants. But, in the second place, it might be possible that the green constituents were not integral elements of the animal, but foreign bodies

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living within it—commensals or 'messmates,' as they are called. Kleinenberg's observations on *Hydra viridis* are decidedly favourable to the former of these views; Schulze's statements as to *Vortex viridis* are equally positive in favour of the second. For he expressly declares that the chlorophyll bodies of this worm are true cells, unlike those of plants; that they divide and multiply spontaneously, which the chlorophyll bodies do not; and finally that they are in some individuals wholly wanting. The importance of these arguments is increased by other facts. It is known that most of the Radiolaria invariably bear in their body certain peculiar particles known as

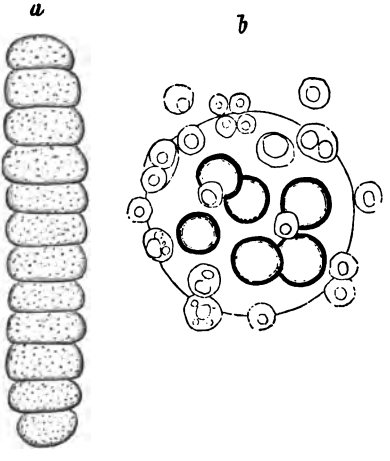

FIG. 18.—*Collozoum inerme* (Haeckel), a Radiolarian forming colonies. *a*, a colony; *b*, a solitary individual, or, more correctly, the internal vesicle of one (the shaded bodies are globules of fat, the outer spots indicate the numerous yellow cells).

the yellow cells (fig. 18), in which a few starch-grains are always present. These yellow or sometimes green cells occur in many fresh-water Radiolarians which have lately been often made the subject of minute investigations. From these, above all from the very careful labours of Cienkowsky, it has recently been proved that these yellow cells in the Radiolarians are in fact nothing more than one-celled Algæ living as messmates with the animal in the same sort of community as certain Fungi and Algæ which, as is well known, combine to form the apparently

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simple vegetables known as Lichens, which, however, are still generally classed as a distinct group of plants. It may at first sight seem somewhat bold to assume that living plants, even of the simplest conceivable structure, could constantly, or almost constantly, be so associated with an animal as to seem one of its histological elements. But this hypothesis assumes a high degree of probability when we remember that numerous parasites occur with unfailing regularity in certain organs of every individual, or nearly every individual, of a

FIG. 19.—Longitudinal section of *Sphenopus Steenstrupii* S. The skin of the creature, *ep*, which is thinnest above, has agglomerated grains of sand throughout its substance.

species—for instance, the larvæ of certain Nematodes in the foot of the common snail; when, moreover, we take into consideration that different animals, more particularly Sponges and Polyps, frequently take up dead or living foreign bodies and utilise them as normal elements of the tissues (fig. 19).

Of course no decisive answer can be arrived at by this method, and only experiment can find one. But it seemed to me to be advisable to state both these possible solutions, and to bring forward those facts which may perhaps soon require us, if

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we find true chlorophyll in animal tissues, to recognise in its presence a singular and interesting case either of parasitism or of the community of two organisms so different as an animal with true tissues and organs, and a one-celled plant.[18]

The general relations between light and the vital activity of animals.—By far the larger number of animals are conscious of light by means of the eye only. This was directly proved by the interesting experiments of Lister and Pouchet, which will be more fully described further on. The commonest effects of light, of its different degrees of intensity, and of its total absence are familiar to all. They are exhibited every day in regular succession in every animal that lives; darkness induces sleep in diurnal animals, and with this are connected certain other effects on some of the organs and their functions; for instance, the amount of carbonic acid exhaled by the Mammalia during sleep is different from that exhaled when they are awake. These proportions, however, are of no particular interest in this place. What is far more important is the observed and well-ascertained fact that all active diurnal creatures fall asleep promptly during an eclipse of the sun; the darkness deceives them as to the hour, and so interrupts the periodicity of their vital activity. But all animals do not react in the same way under the alternation of light and darkness; while some—the diurnal animals—go to rest at the approach of night, others, nocturnal animals, then rouse up, and we might be tempted by this to divide them into day and night animals. But such a division has merely a biological value, for we know that it is in no way co-extensive with the conditions of affinity in animals. We are acquainted with diurnal and nocturnal species among the Mammalia as well as among Birds; some Butterflies, Beetles, and other Insects are nocturnal, though the greater number fly by day; nay, even within the limits of quite small families or even genera, there are some species which are lively by day and others by night. To give one example only: every entomologist knows that night-flying Lepidoptera, nocturnal as to their affinities and structure, as, for instance, the *Sesiæ* or *Aglia Tau* and others, rest by night and fly gaily about by day to seek food or to seize the female. The causes of these

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differences in the mode of life of related forms are entirely unknown, and at the present time it seems impossible even to suggest any hypothesis which would refer such changes in their mode of existence to any sufficient causes.

By far the larger proportion of nocturnal animals, although they are quite lively even in the darkest night, have eyes quite as good and perfect as those of the diurnal animals. Although, as a fact, here and there—as, for instance, in nocturnal birds—certain differences have been observed in the structure of the retina (M. S. Schultze) which might be hypothetically connected with its exceptional functions or with the exceptional time at which they are exercised, yet these investigations supply us with no answer, not even a hypothetical one, to the question as to why certain animals, provided with organs of sight, fly exclusively by night. If we remember that even in the darkest night a certain amount of light always reaches the earth, we might certainly propound the hypothesis that this minute proportion of light suffices them for seeing clearly by. But this hypothesis would give no true explanation of the observed facts; this could only be given if it were possible to compare the differences in the structure in the retina of diurnal and noctural animals with direct reference to the scale of intensity of light to which they are exposed. A circumstance which is more important, because it is directly referable to certain vital relations of animals, is the occurrence of half-blind or wholly blind animals in spots where the light of day cannot penetrate, such as deep caverns, the internal parts of larger animals, and the deepest parts of the ocean or of large fresh-water lakes. The blind crayfish of the mammoth cave in Kentucky is well known, as are also the blind Fishes, Insects, Crabs, Amphibia, and Mammals (moles) of the old and new worlds, and it seems unnecessary to give a complete list of such cases in my text.[19] These familiar facts have hitherto been, and must still be, regarded as so many instances, sufficiently proving the statement that total darkness gradually destroys the eyes of animals originally possessing them; for, since these organs are absolutely useless in such circumstances, in the course of generations they must gradually disappear, according

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to the law of degeneration, in consequence of their disuse. This explanation, it is obvious, presupposes that such blind animals are descended from a parent form that could see; and it cannot be denied that many of the facts hitherto ascertained seem to justify this view. Some of the so-called blind animals are not, accurately speaking, sightless; thus the blind Proteus (fig. 20, *a*), an Amphibian of the caves of Carniola, has an eye deeply seated in the head and entirely covered by the skin. The structure of this organ is very remarkable; it possesses all the characteristic parts of the eye, but they have been arrested at an almost embryonic stage, with the exception of the crystalline lens, of which every trace is absent (fig. 20, *b*); the pigment-layer of the retina is scarcely coherent, and consists of only a few scattered pigment-cells. We may therefore be very doubtful as to whether this Proteus can receive a clear image of the objects that surround it even in a place where there is light;

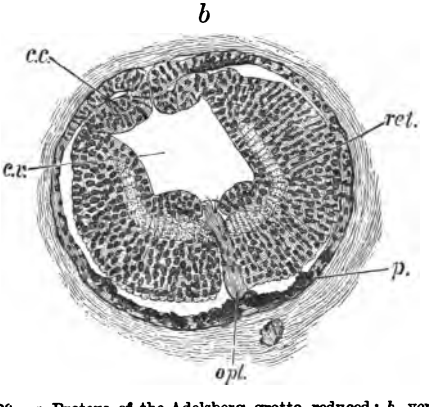

FIG. 20.—*a*. Proteus of the Adelsberg grotto, reduced; *b*, vertical section of the rudimentary eye; *opt*, the optic nerve; *cc*, corpus ciliare retinæ, the inner portions of which meet in front because the lens is absent; *cv*, the internal cavity of the eye without any vitreous humour. The cell-layers of the retina (*ret*) are unusually thick; the pigment-layer, *p*, very slightly developed.

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but certain observations, which I have made on a family of Proteus that I have kept for four years, incontrovertibly prove that this creature is highly sensitive to diffused daylight. As this contains no heat-rays, the eye of the Proteus can receive no impression but that of light. Now it is impossible to suppose that the eyes are now first developing in an originally blind Amphibian which, like the Proteus, lives in total darkness; for even if such an organ could originate under such circumstances it could never become permanent in the struggle for existence, because it could never be of any real use in that struggle. The contrary hypothesis, on the other hand, that the rudimentary eyes of the Proteus are a degenerate form of the more highly developed eyes of its progenitors, seems perfectly natural when we remember that all the other amphibians have highly developed eyes, and that these, when they come to the light from time to time, use them to very good purpose.

The Mole offers another familiar and even better example. This animal, whose peculiar habits are known to everyone, has true eyes, from which none of the essential parts of the eyes of the Vertebrata are absent, although these parts are all of the simplest, almost of embryonic structure. The whole eye is very small, deeply imbedded in muscles, and quite covered by the skin, so that it is quite invisible externally. The lens consists of a very small number of minute and little altered embryonic cells; the retina, in the same way, is much simpler than in the eyes of other Vertebrata. True degeneration, then, such as makes the eye incapable of seeing, has not taken place; nevertheless the eye of the mole is reduced to almost total inefficiency even when by chance it has an opportunity for using it. This almost total blindness in the mole is the result solely of complete degeneration of the optic nerve, so that the images which are probably formed in the eye itself can never be transmitted to the animal's consciousness. Occasionally, however, the mole even can see a little, for it has been found that both optic nerves are not always degenerate in the same individual, so that one eye may remain in communication with the brain while the other has no connection with it. In the embryo of the

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mole, however, and without exception, both eyes are originally connected with the brain by well-developed optic nerves, and so theoretically efficient. This may indeed be regarded as a perfectly conclusive proof that the blind mole is descended from progenitors that could see; it would seem, too, to prove that the blindness of the fully grown animal is the result not of inheritance, but of the directly injurious effects of darkness on the optic nerve in each individual.

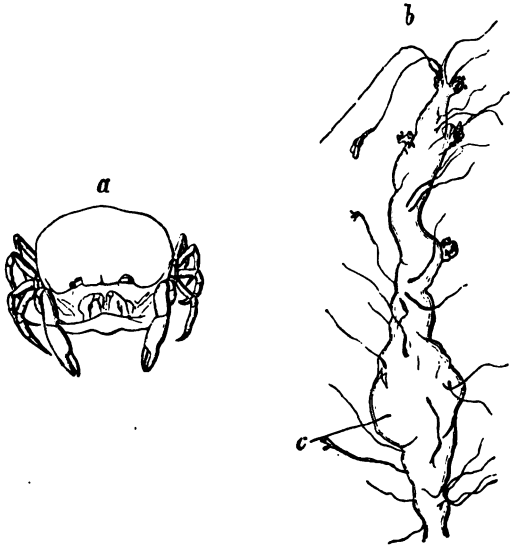

FIG. 21.—*a*, *Pinnotheres Holothuriæ* of the natural size; *b*, degenerate water-lungs, with the distended portion, *c*, in which a small Pinnotheres is established.

To these examples I will add one more which I myself have studied. There is a peculiar family among the crabs, the Pinnotheridæ, of which various species live in the branchial cavities of many Mollusca; some live in Serpulæ, and others (fig. 21) which I have found off the Philippine Islands live in the water-lungs, as they have been called, of Holothurians. These are elongated branched tubes in direct communication with the terminal intestine or cloaca, so that parasites can enter them

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only by the anus; but when the young larvæ of the Crustaceans have once found their way in—which is not difficult by reason of the strong and rhythmical indraught of water through the cloaca—they never seem to quit the situation of their own choice; at the same time they greatly irritate the organ, and as they grow they stop up the tubular vessel more and more till at last serious degeneration of the organ is induced (fig. 21, *b*). The main trunk is greatly distended, while the lateral branches, which usually form a highly ramified structure, dwindle altogether, and are visible only as thin filaments, sometimes feebly branched. The young larvæ now produced are excluded, and become wandering bodies, in obedience to the law which

FIG. 22.—Zoea stage of the larva of *Pinnotheres Holothuriæ*.

governs all Ento-parasites; this they do under the form of the larva, or Zoea (fig. 22), which is common to all crabs, and they have the well-developed eyes of the typical character. Even when they enter the animal, they still preserve these eyes; but as they grow they gradually become blind or half-blind, the brow grows forward over the eyes, and finally covers them so completely that, in the oldest individuals, not the slightest trace of them, or of the pigment, is to be seen through the thick skin; while at the same time the eyes seem to undergo a more or less extensive retrogressive metamorphosis.

The instances here adduced show very clearly that the absence of light sometimes occasions degeneration from disuse,

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and that this occurs to each individual separately within the period of its separate life. These, however, as every zoologist knows, are not the only cases. Most of the blind Parasitical Crustacea now extant have larvæ with well-developed eyes; the young form of many worms, Parasites on Mollusca, &c. (Trematoda), can see, though the adult individuals are blind. In the greater number of these cases—as, for instance, in all internal parasites—we must refer the loss of sight to the same above-mentioned cause, namely, disuse of the organ.

But though we are thus fully justified in saying that darkness so complete as not to allow of the eyes being used at all has in most cases exercised an injurious effect on their existence and structure, it would nevertheless be wholly false to assume that the lack of light must necessarily lead to total or partial blindness. We know of a number of facts directly opposed to such a conclusion. Among the numerous cave-insects there are many which have well-developed eyes, and yet inhabit the same spot as blind species. In some caves in the Philippines and the Pelew Islands which I myself explored, I found, in spots where the most absolute and total darkness reigned, only insects with eyes; *Hadenœcus*, a species of grasshopper which lives in the caves of Kentucky, has well-developed eyes like other animals found there at the same time.[20] Why should not darkness have had the same effect on these animals as on others which have in fact become blind? It might be said—in fact it has been said—that the cave-animals which can see have migrated into the cave only within a short period, and have not been exposed to the influence of the darkness long enough to suffer; while the blind or half-blind, having entered the caves at a remote period, have lost the use of their eyes, wholly or partially, in consequence of long desuetude. But this explanation contradicts the fact previously mentioned, that every mole, Pinnotheres, &c., originally had eyes apparently capable of further development, and of perfectly fulfilling their normal function; and that the influence of darkness is proved to be direct in each individual, and not hereditary. This explanation is also quite decisively contradicted by a fact which is little known generally, and even among zoologists is familiar

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to none but entomologists. I owe my own knowledge of it to my friend Dr. Hagen of Cambridge, U.S. In all the species of the cave beetle, *Machærites*, the females only are blind, while the males have well-developed eyes; in spite of this they both live together in absolute darkness. This proves that the same result—total blindness—may come from different causes; for we may fairly regard it as impossible that in the last-named case the darkness of the cave has affected the females alone, and been ineffective on the males; hence the

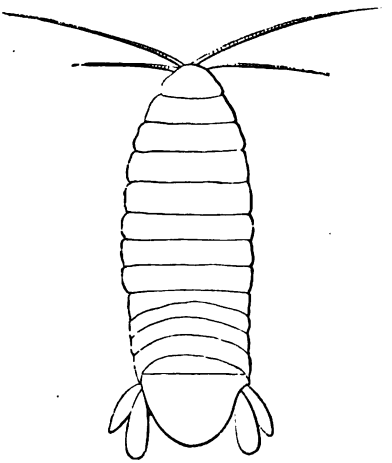

FIG. 23.—Blind Cymothoe in fresh water (small pools) at Pelelew, Pelew Islands. About ten diameters.

blindness of the former cannot be caused by the darkness. In confirmation of this statement I may also adduce the fact that there are many blind or half-blind animals which live in well-illuminated situations, where the moderate intensity of the light would allow them the full use of eyes; this is the case, for instance, with many Bivalves—all fresh-water bivalves and many sea bivalves—with various Annelida (*Chætogaster*), Crustacea (*Cyclopidæ*), and others. I myself have found a perfectly blind small species of Cymothoe (fig. 23) living in slightly brackish water in a basin overshadowed by limestone rock, but

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in spots where full daylight could penetrate. Thus we find ourselves driven, by the facts here adduced and numberless others, to this question: What are the various causes which can, or must, first occasion eyes to be developed, or conduce to their preservation or destruction? A precise answer to this question, unfortunately, is impossible in the absence of all experimental data; but we, as zoologists, may allege the difficulty—indeed, the impossibility—of such experiments, as a sufficient excuse for their never having been hitherto carried out.

In cases like this, where we are not in a position to treat a physiological question experimentally, we must be allowed to construct a hypothetical explanation of the observed phenomena. I therefore consider myself justified in mentioning a very pregnant hypothesis, which was put forward some little time since to account for the presence of animals that can see in the deepest parts of the ocean, where positively not a ray of light can penetrate from above.

It is not very long since it was universally believed, in accordance with the too rapidly drawn inferences of Edward Forbes, that all animal life ceased on the floor of the ocean at the level where rays of light cease to penetrate (at a few hundred mètres). But it is now well known that even highly developed animals live at the enormous depth of from two to three thousand fathoms in both the Pacific and Atlantic Oceans. We have become acquainted, principally through the incessant labours of English, American, and Norwegian naturalists, with a wonderful deep-sea fauna, showing the same striking mixture of blind and seeing animals as the fauna of the caverns.[21] This case is all the more puzzling, because the chief part of such deep-sea animals as can see are extraordinarily unlike their nearest congeners living at the surface and in the light, so that we are forbidden to suppose that they may be species that have only lately migrated from the surface to great depths; indeed, it admits of scarcely a doubt that the deep-sea animals that can see are very ancient forms, the survivors of past geological periods. MacCulloch and Dr. Coldstream suggested a pleasing hypothesis in explanation of these striking facts, which was afterwards taken up and extended by the naturalists of the

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'Porcupine' expedition (1869–70). This hypothesis, which is known as the Theory of Abyssal Light, consists essentially in the idea that the light diffused by phosphorescent creatures is capable of taking the place of sunlight in those depths which the rays of the sun cannot penetrate. It is evident that the correctness of this idea cannot possibly be experimentally tested and proved, but at the same time we cannot but admit that it is highly probable. For although it has been argued, as an objection to this idea, that phosphorescence is not an exclusive peculiarity of deep-sea creatures, but on the contrary, so far as we know, occurs more frequently among animals living on the surface, this objection must certainly be considered as anything but conclusive. We know from exact experiment in individual cases, particularly on glowworms, that phosphorescence is the product of a chemico-physiological process in the living body of the animal, exactly as carbonic acid is a natural product of respiration. What requires us to assume that this ought to occur in deep-sea animals only,[22] supposing that theory to be accurate? The obvious ground of this objection is the tacit assumption that, if phosphoric light can really be of use to any creature, it must only occur in cases where it could be utilised. But this mode of argument offers an example of a very common but very gross error: the idea, namely, that the effect produced by the function of an organ, or that the function itself—in the present instance the production of light in the light-organ—can be brought into existence by reason of the usefulness of its results, when the use, in fact, makes its appearance at a later period. Phosphorescence, as it is developed in the living tissue of animals living at the surface, may perhaps never be of any use to the creatures that possess it, nor to the enemies that pursue them. But the same effect of a similar chemical process may nevertheless be advantageous to other creatures, which, like the deep-sea animals, would otherwise be condemned without exception to live in total darkness. We are not at present acquainted either with the various chemical processes by which phosphoric light is produced in different animals, nor with the uses which these processes may subserve for the animals themselves; but we know of some

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animals, at least among the insects, to whom this light serves as a guide by which to find each other, as in the male and female *Lampyris*; and such a light would undoubtedly be equally serviceable at the bottom of the sea to all the animals, those preying as well as those preyed upon; for without light, escape and pursuit must alike depend wholly on accident, and the remarkable fact that the eyes of deep-sea creatures are not always and completely abortive would thus be accounted for, as far as is possible perhaps on the whole.

One pressing difficulty, however, remains. We know that blind animals, as well as those that can see, exist at the bottom of the ocean, while their nearest allies at the surface have well-developed eyes. Why have the deep-sea species lost their eyes? The same question confronted us with regard to the cavern animals, and could not be answered even hypothetically. With regard to the deep-sea animals—more accurately deep-sea fishes—Dr. Günther, in London, has lately made a remarkable attempt to explain the case, and although his views are as yet unpublished he has been so amiable as to communicate to me their most essential features. He has found, particularly among the deep-sea fishes brought back by the 'Challenger' expedition, certain very peculiar forms, blind and not-blind; the latter have exceptionally large eyes, which seem especially fitted to absorb pale phosphoric light in large quantities, while the blind fish, on the other hand, are distinguished by peculiar and sometimes colossal organs on the head, which have quite displaced the eyes, and which exhibit a very singular structure, that justifies us, according to Dr. Günther, in assuming that they are peculiarly and strongly developed phosphorescent organs.[23] Now these, in Dr. Günther's opinion, may very possibly be used by their owner, as torches and other lights are used by fishermen, to entice and catch other fish. But, just as pirates are attracted by the lights of fishermen and guided to their victims, so the light which these blind fish carry in the two lanterns on their head to attract their prey may be a beacon to their enemies, and at the same time be of assistance to such fish as can see, in their movements generally. Thus we can well understand that in the struggle for existence, which

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must of course have been carried on among the various creatures on the floor of the ocean, every form having small eyes or small illuminating organs, being unable to see clearly or to give enough light, must soon have been exterminated, while none but the most extremely developed species could hold their own in the struggle. Newly introduced varieties must therefore have been able to develope either larger eyes and keener vision, or else strongly illuminating organs, in order to escape annihilation. This evidently presupposes that the lantern fishes of the ocean-depths, being blind, must have other means for distinguishing and identifying the prey or the foes that approach them; and this seems in fact to be the case, for from their proboscis or muzzle depend long feelers, beards, and the like; and at their tips or bulbous ends, organs of touch or of smell might easily be situated, which could serve such a purpose.

Special instances of the influence of light on animals. There are numerous special influences exercised by the different degrees of intensity of light or by its periodical changes on the different functions of the animal organism; but those only interest us which may now be regarded as directly connected with the fitness for life of a species under certain external conditions of existence. Thus we may entirely leave out of consideration the influence, for example, of red light on the formation of carbonic acid during respiration, the difference of the amount of carbonic acid exhaled by day and by night, and others; although these processes are of the utmost importance for the life both of the organs and of the animals. If we thus dispose of these and other similar effects of light, there remain two points which we must discuss; the first being the presence or absence of pigment in the skin of the animal and the *chromatic function*, as it is termed.

All animal pigments in the skin were formerly regarded as arising from the direct influence of light upon the skin, and, as a necessary corollary to this view, it was also asserted that the absence of light always prevented the formation of such pigments, or destroyed that which was already formed. The fact that the greater number of cavern animals and almost all

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ento-parasites are quite, or almost quite, white, appears a striking proof of the accuracy of this statement. Even as lately as 1870 it was asserted by the celebrated French député and physiologist, Paul Bert, that the larvæ of the well-known Axolotl (fig. 24) were incapable of forming pigment when they were brought up under the influence of yellow light, and he unhappily designated this absence of the epidermal pigment as 'etiolation.' This term, as is well known, has a fixed signification in the physiology of plants; it is exclusively used to

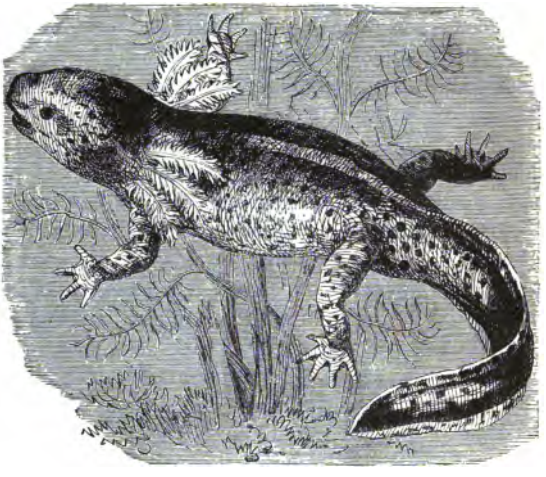

FIG. 24.—*Siredon pisciforme*, the Mexican Axolotl.

designate those cases of the absence of the green hue in plants which, having grown in the dark, have been checked in the formation of the chlorophyll-bodies, which are the organs by which they assimilate and elaborate their nutrition; at the same time, as the light is no longer able to act as a check on their excessive growth, the leaves and stems become much elongated and acquire a yellowish-white hue, all of which phenomena can be easily observed in the shoots and leaves of potato tubers which have begun to sprout in a cellar. In the cases of so-called 'etiolation' described by Bert as occurring in

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the larvæ of the Axolotl, on the contrary, in the first place, no abnormal growth was observed as a result; secondly, it must be strenuously disputed whether animal pigment is in fact capable of 'etiolation;' for it is certainly not, like chlorophyll in plants, an *organ* capable of decomposing carbonic acid under the influence of light. Thus the term was decidedly misapplied by Bert to cases in which the pigment of the skin disappeared under any influence, whatever it might be; whether yellow light or the total absence of light was primarily the cause of the disappearance of the pigment which he mentions, is not clearly stated. We know that in plants all true pigment—not, that is to say, the green of chlorophyll nor the brown and red of xanthophyll, but the true yellow, red, and blue *pigment* of flowers—is formed just as well in perfect darkness as in broad daylight. Tulips, for instance, which are made to bloom in the dark, have a singular effect from the contrast between their brilliant colouring and the shapeless outlines and pale yellow hue of their etiolated leaves. This holds good with regard to most, if not all, animals; they preserve their colour in spite of the more or less complete absence of light, as is proved by the undeveloped young of reptiles and butterflies, chicks, &c.; true deep-sea creatures which live at a depth of from 2,000 to 3,000 fathoms often exhibit[24] colours quite as brilliant as those of animals living at the surface, and it is easily proved by experiment that the larvæ of frogs or the tadpoles of newts develope their pigment quite as rapidly and perfectly whether they are brought up, from the time when they leave the egg, in full daylight or in absolute darkness. The earliest experiments on this subject with which I am acquainted are those of Mr. Higginbottom.[25] Although he does not expressly declare that pigment is normally developed in the dark, it follows from the remarks he makes; and I can myself add the results of investigations pursued during two years, by which I have established that in the tadpoles of our common toads and frogs the pigment is equally well developed in yellow, blue, or red light and in absolute darkness. It is unnecessary to discuss these experiments in detail, for in every case where the other necessary conditions were at their optimum

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the pigment of the skin of the tadpoles was normally developed in every kind of light, as also in the dark.

Thus experiment here confronts experiment. It is not difficult to find an hypothesis to account for this. In none of the experiments hitherto conducted, not even those of Bert, were the heat-rays or the chemical rays excluded from the light falling on the young animals. It may have happened that in the darkness the little larvæ were not supplied with supplementary or even requisite nourishment—in short, it would seem that the absence of pigment observed by Bert in the young Axolotl did not arise from the absence of light, but from the effects of some other cause as yet not ascertained, as insufficient or unsuitable food, the sinking or raising of the temperature, &c ; or it was perhaps a case of true albinism, and thus a form of disease. All who have bred the Mexican Axolotl are well aware that sometimes a white variety—not a true albino—suddenly occurs; but the cause of this variation is at present unknown. Thus Professor Kölliker of Würzburg reared a whole family of these white Axolotls, which, with their blood-red gills, were very beautiful objects; while in my own laboratory, where there is a much greater absence of light than in Kölliker's, I have as yet entirely failed in breeding even one white Axolotl, although during the last six years I have bred hundreds of individuals under the most various conditions of life. I am wholly unable to assign any plausible explanation for this difference, and it is the more striking because the six old specimens, from which I have now had at least six or seven broods, came originally from the same brood as those from which Kölliker has obtained so many white individuals. Finally I can but repeat my conviction, founded on these experiments, first, that we have as yet no suspicion even of the causes which sometimes determine the absence of the epidermal pigment in the Amphibia and other animals (as rats and mice, in which these unknown causes even become hereditary); and secondly, that this absence of colour is certainly not to be ascribed to the absence of light, since we know that animal pigment, like vegetable pigment, can be developed in total

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darkness, and in fact is so developed normally in many animals.[26]

In absolute antagonism to the old hypothesis which ascribes the origin of the pigment in the skin of animals to the direct influence of light, there is another which, under the almost supreme influence of Darwin's theories, is now as generally accepted as the other was formerly. It is now almost universally asserted that the colours of animals have arisen from either natural or sexual selection. We will postpone the discussion of this view to a future chapter, in which the uses accruing to animals from their colours will be considered; but, since it is proved by abundant evidence that at least one particular kind of protecting resemblance—*i.e.* the adaptation of the colour of the skin of certain animals to the colours of the objects that surround them—depends on the influence of light through the medium of the eyes, it will be convenient to treat of it here. Pouchet applied the term 'chromatic function' to that adaptation of colour to the surroundings of the creature which is indirectly the result of sight, in order to distinguish it clearly from other cases in which—so far as we can at present tell—the distribution of colour is not influenced by light at all.

The term 'chromatic function' refers neither to constant colouring, even when this causes a protective resemblance, nor yet to such variations in colour as are occasioned in Chamæleons and Cuttle-fish by physical irritation without any protective resemblance being the result. The expression, which is not altogether a happy one, is new; but the fact it designates, that such protective changes do occur in many animals, has long been known. In the year 1830 Stark made a number of observations on the subject, on species of the genera *Leuciscus*, *Gasterosteus* (the fresh-water Stickleback), *Cobitis barbatula*, and the common Perch, *Perca fluviatilis*. All these fishes change colour with some rapidity, some in a few hours, others in from two to three minutes; and we know now that many splendidly coloured sea-fish have the same power, often in a quite extraordinary degree, as, for instance, species of *Serranus*. Shaw seems to have been the first to observe, in 1838, that such fish as are capable of changing their colour, apparently at will, must be

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more or less protected against their enemies by the resemblance thus caused between the colour of their skin and that of their surroundings. Similar observations were made by Agassiz, Ayres, and Store , on the salmon of the United States, while European naturalists were the first to experiment on Amphibia which exhibit a similar power of assuming a protective hue. Finally, Heincke of Kiel has quite lately published a very careful description of the protective changes of colour[27] in *Gobius Ruthensparri*, which exhibits the most conspicuous variations of colour that have as yet been described.

Before entering on the discussion of those experiments by Lister and Pouchet on the chromatic function, by which we were first enabled to understand the observations above mentioned, it will be advisable to describe the structure of the skin

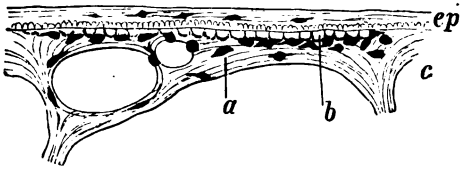

FIG. 25.—Section of a frog's skin. *ep*, epidermis, including five pigment-cells; *c*, cutis with black star-shaped, deep-seated cells; *a* and *b*, a thick single layer of yellow pigment cells close under the epidermis.

and the mode of distribution of the pigments in it. One example—the skin of the frog—will suffice for all cases. The skin (fig. 25) consists of two distinct portions, the epidermis and the cutis. The former (fig. 25, *ep*) is entirely composed of cells, and the innermost layer contains cylindrical cells; the cutis is chiefly fibrous and encloses nerves, large cavities for glands and cell elements. These last are commonly filled with pigment, and the remarkable changes of colour in the frog's skin depend entirely on the distribution of these highly ramified pigment-cells and their power of shrinking under certain kinds of irritation. The pigment in these contractile cells—known as the chromatophores—is different in different individuals and in different parts of the body, yellow, brown, black, sometimes even red or green. Besides, the colour of the chromatophores varies

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with the state that they happen to be in, and differs during contraction and expansion. Heincke, for instance, has shown that in *Gobius Ruthensparri* the chromatophores that are yellow or greenish yellow when distended become orange-coloured when contracted; while the orange or red ones when shrunk become brown or even black. These (so to speak) *active* movements of the chromatophores were observed before by Lister, whose careful drawings of the chromatophores of a frog have been copied in the accompanying woodcut (fig. 26); it is hardly necessary to remark that the studies of the various

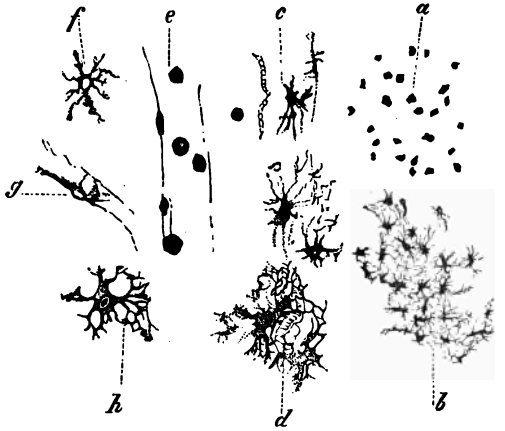

FIG. 26.—Chromatophores from the skin of a frog, copied from Lister. *a*, wholly contracted; *b* and *c*, half relaxed; *d*, wholly relaxed; *e*, wholly contracted, a capillary vessel; *f*, *g*, *h*, expanded colour-cells or chromatophores.

stages of contraction were made from the chromatophores of living animals, and in fact it is quite easy to repeat these observations on the extended web skin of a frog's foot.

These chromatophores are distributed in the skin with a certain regularity; in this particular, reptiles, fishes, and amphibians show hardly any—or no—difference. They usually occur in the cutis only, but sometimes they penetrate into the epidermis, as, for instance, was the case in the section of the skin of a common frog, shown in fig. 25; but it is not known whether they then retain or lose their contractility. Sometimes the epidermis-

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cells are all supplied with pigment, as in many reptiles, but these certainly are not true chromatophores, and so are incapable of occasioning any change of colour in the skin; but of course their constant hue must affect that of the skin generally, as well as the marking produced by the more deeply seated chromatophores. The true chromatophores lie in different layers in the cutis; close to the epidermis, light-coloured yellow cells occur, beneath them the red or brown, and, in the deepest layer, the black. In some spots the pigment-cells of one kind or the other may be wholly wanting; sometimes the black ones form a close mass in one spot, while in others the red or yellow predominate, but very few spots are devoid of pigment altogether. It is on this distribution and stratification of the chromatophores and their alternate expansion and contraction that the pattern (so to speak) depends which the frog's skin displays at any given moment. If all the chromatophores are relaxed, brown or black will predominate, and in the spots where light-coloured chromatophores lie in patches their hue will be dulled; if they contract while the light ones are still extended, these latter will be more conspicuous. Heincke detected in *Gobius Ruthensparri* yet another kind of chromatophores, which were filled with iridescent crystals of marvellous delicacy; they are visible, according to the degree of contraction, as spots of metallic sheen, or are altogether invisible.

The property on which the contractility of the chromatophores depends is at present unknown, although various hypotheses have been suggested in explanation of it. It is of little importance for our purpose to learn which of all these antagonistic hypotheses will ultimately be proved to be the right one, since we know that all living protoplasm is essentially contractile, and moreover that all cells devoid of membrane—like the young ovum-cell, the white corpuscles of the blood, and others—sometimes possess this contractility in a very high degree. And the chromatophores belong to the class of cells without membrane; hence we need not be surprised to find that they contract like other similar cells.

It was formerly supposed that the exciting agent which gave rise to the contraction of the chromatophores must act upon

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them directly, so that variations in the intensity of the light, warmth, &c., could not produce contraction, or, on the other hand, expansion, unless they were under the direct influence of the rays. Some observations certainly have been made, particularly those of Wittich, which prove that in animals having the chromatic function (as the frog) the direct effect from light-rays is, in fact, perceptible in a small degree; but it is now definitively established that this is not generally the case, and that the changes of colour thus produced cannot be included under the term 'chromatic function,' since no adaptation of colour to the surroundings is effected by them. Lister demonstrated, on the contrary, by his experiments on frogs, as long ago as 1858, that the activity of the chromatophores in cases of chromatic function depends solely on the healthy condition of the eye. So long as the eyes are in connection with the brain by means of the optic nerves, the light reflected from surrounding objects has a marked effect on the chromatophores; but, so soon as the eyes are destroyed, or the optic nerves are divided, the chromatophores also become totally incapable of perceiving any variations in the intensity of light and colour; thus the light reflected from objects can only affect the colour of the skin by the interposition of the eyes.

These observations were subsequently repeated by Pouchet, who evidently was not aware of the preceding experiments, on Fishes and Crabs; and he, like Lister, came to the conclusion that the irritation which excited the action of the chromatophores took effect only through the eyes and optic nerves, and not directly on the pigment-cells. Among the numerous new instances which he brought forward, some of them highly instructive, the case of a plaice observed by him is particularly interesting. These fish have, as is well known, a white side which constitutes the under surface, and a parti-coloured side which lies uppermost; this upper side exhibits the 'chromatic function' in a very high degree. Among a great number of normal specimens of the species which, on a white sandy bottom, were also whitish or very pale-coloured, he met with one single dark-coloured fish in which, of course, the chromatophores must have been in a state of relaxation, and this specimen was

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as distinct from its companions as from the bottom of the aquarium. Closer investigation proved that the creature was totally blind, and thus incapable of assuming the colour of the objects around it, the eyes being unable to act as a medium of communication between them and the chromatophores of the skin.

Up to this point Pouchet's researches present nothing really new. But he proceeded to investigate the natural question: How and by what course is the impression received by the eye passed on from the optic nerve to the chromatophores located in the skin? Two modes of transmission are here possible: one by means of the spinal cord and the pairs of nerves distributed by it to certain sections of the muscles and skin—these are known as the spinal nerves; the other by two nerves running longitudinally close to the vertebral column, the sympathetic nerves, as they are called, and which are closely connected with the spinal nerves and the brain. Pouchet detected and proved that the connection was not severed, and the chromatic function was not interfered with, if the spinal cord was completely divided close behind the brain, thus cutting off the first means of communication between the eye, the optic nerve, and the chromatophores. On the other hand, the chromatophores lost their power of contraction completely if the two sympathetic nerves only were destroyed at the root. These, as before explained, are connected with the very finest nerves of the skin —which, it would seem, extend to the chromatophores—by means of the spinal nerves which are given off from the spinal cord on each side at regular intervals. By severing the connection of some of these with the sympathetic nerve of the same side, Pouchet succeeded moreover in limiting the chromatic function to those spots where the nerves remained in communication with the sympathetic; and he was thus enabled to produce at pleasure a zebra-like marking on one side of a fish, while the other side retained its natural hues and their normal variation according to the colours reflected from surrounding objects. In this way it was indisputably proved that the sympathetic nerve, and not the spinal cord, is the conductor of the optical stimulus which causes the motions of the chromato-

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phores; and we may now venture to attempt to investigate how it is that an adaptation to the colour of surrounding objects can be effected by these variations in the colour of the skin, that are only indirectly dependent on the light.

Professor Dewar has recently shown [28] that the different colours of the spectrum influence the eye and the retina in very different ways by producing an electric current which has been termed the 'optic current.' The intensity of this current, according to Dewar, is greatest under yellow light, weakest under purple light, and nil in total darkness. Of course we cannot directly compare the stimulus which is communicated from the rays of light through the optic nerves to the sympathetic nerve, and then by way of the spinal nerves to the nerves of the skin, and finally to the chromatophores, with this 'optic or retinal current,' because an electric current invariably takes the shortest road, which the nervous irritation above described certainly does not. But if we assume that the measure of the force exercised by the eye on the chromatophores may be approximately estimated by the force of the retinal current, an explanation of the phenomena of the chromatic function would be easily found.

Every object reflects the light according to the nature of its colour; black surfaces, when they are not too smooth, absorb the rays in the highest degree, red come next in order, and then yellow. White reflects nearly all the rays; hence a black background, reflecting but little light, will stimulate the eye in a very faint degree, and the excitation, analogously to the ascertained working of the retinal current, will apparently not be strong enough to occasion the contraction of the black chromatophores; these remain expanded, and give the skin a dark hue. If the light is reflected from a red or blue object, the somewhat stronger stimulation causes the black or brown chromatophores to contract while it does not affect the red or yellow ones; the animal then exhibits a reddish or bluish tint. The light reflected from green or yellow bodies produces a still stronger effect on the chromatophores, till a pure white light makes all the inmost layer of the chromotaphores contract, and the animal is almost colourless. This explanation coincides perfectly with Pouchet's observations, though Heincke certainly makes

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a few contradictory statements. He says that when a *Gobius Ruthensparri* is placed on a red bottom the yellow chromatophores shrink as well as the black ones, although the yellow contract less strongly than the latter; but, according to Pouchet's explanation, the yellow chromatophores should hardly or never contract under a red light, since it is incapable of affecting even the red chromatophores. This indicates that there is still much to be done in this enquiry; and it is to be hoped that naturalists who take an interest in the subject and are in a position to make independent investigations will not suppose that it is exhausted even after the interesting and extended experiments of Lister and Pouchet.

We must also guard against the idea that another question which is connected with this has been in any way answered: namely, that as to the first formation of the pigment in the chromatophores—a question which is often, but erroneously, regarded as identical with the other: How a particular mode of coloration, or rather of distribution of the pigments, is to be accounted for. This has, in fact, been fully explained by Lister and Pouchet in the case of chromatic function, but it is clear that the other question is not touched by it; for chromatophores, *i.e.* dermal cells characterised by a rapid and peculiar contractility, must have existed before the contractions occasioned by the light reflected from surrounding objects could result in a useful function. The permanence and even the further development of the chromatic function in such animals as most required its protective effects is of course easily explained by the principles of the Darwinian theory—by natural selection in the struggle for existence; but its first occurrence depends exclusively on the pre-existence of pigment in highly contractile cells.

The contractile power of the chromatophores, however, offers no special difficulty, as has already been observed, since we know that protoplasmic cells, devoid of an enclosing membrane like those of the chromatophores, are universally endowed with this property; any such cell, being a cell of the connective tissue of the cutis, might become a chromatophore, if pigment-granules were deposited in its protoplasm. Thus the only

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final difficulty is the indispensable pre-existence of the pigment. Whence and how does pigment originate? Recent Darwinian views no more supply the answer to this question than the older theories of the origin of colouring-matter through the direct influence of light. It is incontestably certain that light alone cannot give rise to a pigment, as was formerly supposed; and it is very probable that, even if the production of darker colouring sometimes seems to depend on the influence of light, it is to be attributed to the chemical rays or heat-rays which are always associated with light-rays. It is equally certain that all the peculiarities collectively which make animal pigments useful to the owner do not make their existence indispensable; so that the chromatic function, in this special case, explains only the various arrangements and rearrangements of pigment already existing, but can throw no light on the obscurity which shrouds the existence of these chromatophores, however great the utility they may acquire, and undoubtedly possess, by the nature of the different pigments they may contain and by their distribution and dependence on the eye and the optic nerve.

The question remains equally unsolved with reference to all other kinds of animal colouring. They may, as in the chromatic function, be elicited and influenced by the indirect action of the light, or they may, as is now very generally assumed, have originated by natural or sexual selection;[29] but these causes are still inadequate to the production of the pigment itself, when we think of its *origin* irrespective of its *distribution*. The eye was not formed by the faculty of sight, although, when once it was formed, it was largely modified by the function; the eye must have existed before it could be used. The same is the case with regard to the pigment. I lay some stress on this comparison, because it is so common to find it stated in popular treatises, nay, often enough in scientific works, that this or that *colour* is the result of selection or of adaptation, the word 'colour' being no doubt used by many of the writers instead of the more correct expressions—colouring, pattern or arrangement of colour. The answer to this ultimate query—How the pigment was first formed—cannot at present be given; and although many experiments and observations

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have already been made which indicate the possibility of an early solution of it, they are at present far from being perfect enough for us to discuss them in this place. One thing only may here be briefly observed. If the Darwinian principles are indeed the true ones, we must assume that the pigment itself—not by its variable distribution—together with its subsequently acquired utility in the maintenance of the species by the selective influence of the conditions of life, must either have some direct primary function in the normal life of the individual, or else be the inevitable secondary product of some indispensable physiological process. In a few rare cases this last is known to be the case, and they have been classed by Darwin as cases of correlational colouring. But we may hope that the time is not far off when the presence of every kind of pigment will be as intelligible to us—as easily referred, that is, to definite causes—as are certain variations of colour, which, under the chromatic function, are now recognised as being directly and absolutely dependent on the effects of light on the eye of the animal.[30]

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CHAPTER IV.

THE INFLUENCE OF TEMPERATURE.

THE sun, the source of light, supplies other powerful stimuli to organic life on our globe. All the heat which influences the development and continuity of life either is now, or formerly was, derived from the sun, in whose rays light- and heat-rays exist in combination. The influence of the heat-rays only, on animal life and on its distribution on the globe, will form the subject of the present chapter.

It must be almost superfluous to bring forward any special facts to prove that heat, or the degree of temperature at a given time, has a marked influence on the life of animals and on their vital functions. Everyone knows that perspiration, *i.e.* the action of the sweat-glands in the skin, increases as the temperature rises; and that a considerable heat must be kept up if a hen's egg is to be perfectly developed or hatched. The heat which reigns during summer in the Eastern States of America, in Madrid, Naples, and other places, is often intimately connected with fatal epidemics, nay, sometimes is productive of them. Most Europeans become indolent and slothful if they are forced to pass the hot season between the tropics or even in Naples or Madrid. The approach of winter, on the other hand, is equally perceptible, and it may be confidently asserted that many millions of human beings make their livings and support themselves solely by the indirect results of this transition from summer warmth to winter cold, otherwise frequently so injurious. If, for instance, we suppose that the thirty or forty millions of human beings who pass through the severe cold of an American winter were by some means relieved of the necessity of buying, say every

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three or four years, a winter overcoat, the necessity for a certain annual expenditure of a sum of certainly not less than a hundred thousand dollars would also be removed, and an enormous number of the population would be thereby deprived of the means of existence. Animals, however, under these circumstances behave very differently; the lower animals, and above all those that live in the sea, are far less dependent on variations of temperature than man and the warm-blooded animals; nevertheless the very simplest of all forms, the Protozoa, are dependent on warmth in a very remarkable manner.

Many of my readers have no doubt been at some time obliged to experience some degree of acclimatisation to a tropical climate. Everyone who has passed some time between the tropics knows that sooner or later he got accustomed to the higher temperature, and at the same time probably lost the good appetite which he enjoyed in his colder native country. He will also have observed that the effect of a high temperature on the action of the sweat-glands and kidneys was different from that of a colder climate. A European sees the natives of a tropical country turn drowsy or shiver with cold at a degree of temperature which, though low in those regions, would, in his own country, have made him wish to fling off his garments and plunge into icy-cold water; but a prolonged residence in the hotter climate will gradually accustom him to the sensitiveness of the natives to small variations in temperature. The natives of Port Mahon in Minorca were excessively astonished at seeing me and two other Germans bathe regularly in the sea in the month of September, although the temperature of the sea-water of the harbour where we bathed was certainly not less than 18° centigrade, and very probably more.

These few facts may suffice; I should not have mentioned them if it had not seemed desirable to make the reader familiar at once with the idea that the influence of temperature on animals depends not merely on the absolute degree of heat experienced, but on the variations of temperature to which every animal, almost without exception, is exposed in the course of its life. The above-mentioned facts prove too that animals are capable of enduring the effects of change of temperature and to

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adapt themselves to it without any change of structure being the inevitable result, although such changes are clearly recognisable in function; and, in the third place, that the same degree or variation of temperature affects different organisms in different ways. We might perhaps be disposed to assume, on the ground of theoretical conjecture, that all the animals living together in the same climate must be affected in the same manner by the normal variations of its temperature; but such an assumption would be, as everyone knows, altogether false. On the contrary, well-known facts tend to show that there are enormous differences in this respect, and the same facts teach us at the same time, that the well-being of animals living in association depends far more essentially on the variations and extremes of temperature than on the absolute degree of heat to which they may be simultaneously exposed at any given time.

The results thus laid down, somewhat dogmatically perhaps—but the reasons on which they are founded will be given presently—justify us (only hypothetically, it is true, for the present) in denying the value frequently attributed, even quite lately, to the curves of temperature as constructed by meteorologists. Annual isothermal (isochimenal or isotheral) curves are constructed by estimating the mean temperature for the days first, then for the weeks, months, seasons, or for the whole year; but these curves calculated from mean temperatures are in truth, if of any, only of very small importance to the matter in hand. Thus, for instance, it is certain that a given degree of temperature, conceived of as absolute in its effects, will have a favourable effect on one animal, while on another it is less favourable or even injurious. Now the mean temperature of a day, as calculated by the meteorologist and assumed as the basis of all his curves, can afford no standard by which to measure the influence of the heat during that day, since it is not the same as any of the different temperatures observed during the day, and that mean of temperature may be the result of very dissimilar extremes. A pond-snail is developed, lives, and feeds best in a mean temperature of about 20° centigrade; but this, as a daily mean of heat, might be the mean of two extremes lying far apart from each other. This water-snail

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does not assimilate its food—that is to say, digest and grow—till the water has attained a warmth of from 14° to 15° centigrade, and it entirely ceases to do so when the water has reached 30° to 32°. Hence it is plain that the pond-snail is for a long time less favourably circumstanced than a bird or mammal living near the pond or in it, and close to the snail; for they, like all warm-blooded animals, can carry on the process of digestion even when the temperature falls below the freezing point or rises above 36° or even higher; the Lymnæa meanwhile is materially checked in its growth, or even killed. Nevertheless the calculated mean daily temperature may be identical with that which would afford the most favourable conditions for the pond-snail. Hence it is evident that a classification of animals according to the climate in which they live in fortuitous community—as those of the tropical, temperate, and frigid zones—has no real value, and is simply an expression of the fact that different animals live in different climates. All such divisions founded on the terminology of meteorology serve only to conceal the true relations of animal life to the temperature that influences it, and consequently cannot be regarded scientifically as either accurate or useful. I therefore shall suggest another method of classification which agrees better with the nature of the relations that can be proved to subsist between animals and those variations of temperature to which they are subjected.[31]

Almost all animals are exposed within the course of a day to more or less considerable changes of temperature. If we assume, as we are justified in doing by certain observations that shall presently be communicated to the reader, that there is a certain degree of heat (which need by no means be identical with the meteorological mean temperature of the day) which is most favourable to the well-being of one or of several species of animals, obviously every rise or fall of temperature above or below this favourable point must be to a certain extent injurious to the creature. The interval between the daily extremes may be great or small without any alteration in the daily meteorological mean; moreover, the favourable temperature—the optimum of temperature for the animal—may either coincide with

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the meteorological mean or lie nearer to one of the extremes—the maximum or the minimum—than the other. We have here assumed that the optimum is the same for all animals; but they may nevertheless be very differently affected by the variations in temperature according to the degree of the variations themselves. Then those animals which can endure the greatest variation in the direction of either extreme evidently exhibit a certain contrast to others which can only thrive under very small departures from the optimum, and their distribution must depend essentially on this characteristic. Certainly the distinction thus indicated cannot be regarded as absolute; but we shall nevertheless do well to avail ourselves of it as a means of classification, and to designate animals, according to Möbius,[32] the former as *eurythermal*, the latter as *stenothermal*.

We also know that the optimum of temperature may be extremely different for different animals, since some exist near the poles and others on the equator, some live on ice and some in hot-water springs. Nevertheless, a rise of temperature above the optimum must in either locality influence the animal in an analogous manner, whether it dwell on the ice of the North Pole, or at the summit of a high peak, or on the scorching plains of the tropics; and a fall of temperature below the optimum must likewise produce analogous, though not identical, phenomena. Hence we may, in a certain sense, assume the optimum of temperature as being the same for all animals as a basis for our discussion of the question: How do variations of temperature affect the animal? and thus we may divide this chapter into three sections, the first dealing with the effects of a falling temperature, the second with those of a rising temperature, and the third with those of an equal temperature, and at the same time with the dependence of animal life on these three conditions—the term 'equal temperature' excluding any great changes whether of rise or fall.

I. The influence of a falling temperature on animal life.—This influence may exhibit itself in many different ways. A small fall in temperature may be as injurious to one animal as a great fall to another, while a third species may be wholly unaffected by either. Animal life is often destroyed before the

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freezing point is reached, while some animals can endure even to be actually frozen up without being killed, their vital powers merely becoming latent. Sometimes the effect of the reduced temperature induces modification of the functions only, sometimes it leads to changes in organic structure. Unfortunately

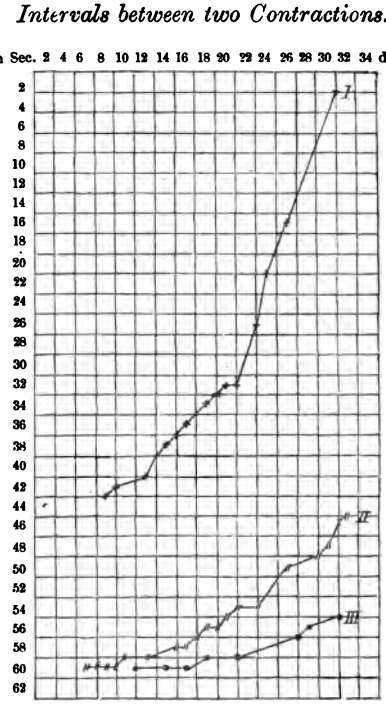

FIG. 27.—The mean thermal curves detected by Rossbach for the contractile vesicle of Infusoria. I. For *Euplotes Charon*. II. For *Stylonychia pustulata*. III. For *Chilodon cucullulus*. The animals are shown in fig. 28.

very few experiments on individual cases have been made which elucidate this branch of the subject, but we will investigate these more closely. A reduction of temperature which never falls so low as the freezing point of fresh water may still, under some circumstances, lead to the suspension of various

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animal functions. Rossbach proved that the rhythmical contractions of the contractile vesicle in Infusoria are very remarkably affected by a low temperature. He found by very carefully conducted experiments (fig. 27) that the pulsations of these vesicles were generally carried on most regularly and rapidly in a temperature varying between 15° and 25° centigrade. But the lower-

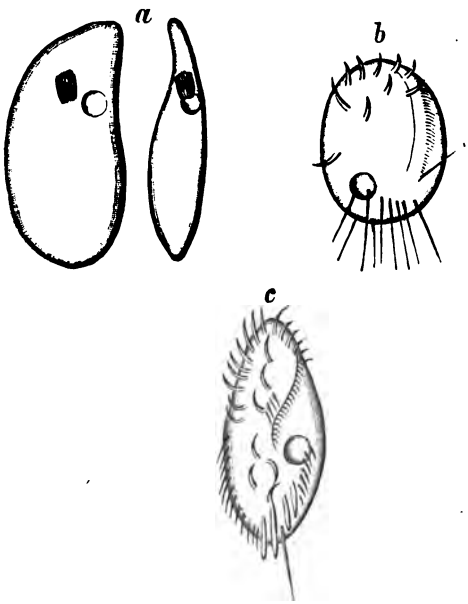

FIG. 28.—The Infusoria observed by Rossbach. *a*, *Chilodon cucullulus*; *b*, *Euplotes Charon*; *c*, *Stylonychia pustulata*. Highly magnified.

ing of the temperature to 5° above freezing point (5° centigrade) has a quite different effect on the different species; thus, at this low temperature the vesicle of *Chilodon cucullulus* contracts seven times in a minute, that of *Stylonychia pustulata* only three times, while at 15° there are fifteen pulsations per minute in each. At 10° above zero * the length of one pulsation in

* Zero, in the centigrade thermometer, is freezing point; 100° the boiling point of water at the sea-level.

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Chilodon cucullulus is seven seconds, in *Euplotes Charon* forty-eight. We see at once by this that the active life of the animal is not suspended even at so low a temperature as 5°; for although the pulsations succeed each other more slowly than at a higher temperature, they occur regularly, and the contents of the vesicle are discharged with the same regularity. But if the temperature is still further reduced to 3° or 2° above zero centigrade, the pulsations of the vesicle, as well as all the movements of the various members of the creature—its cilia, bristles, and so forth—cease entirely; a condition of the animal protoplasm supervenes—which must not be mistaken for death, though it frequently precedes it—to which Rossbach has given the appropriate name of 'chill-coma.' If this chill-coma of the Infusoria is not too long continued, the creature may be revived by raising the temperature; but if it is long continued, or if the temperature is still further lowered, the animal finally dies.

Our common pond-snail, *Limnæa stagnalis*, offers a very interesting example of the influence of cold on the organic functions. I found by experiment that this animal, when young, first begins to assimilate food, and consequently to grow, when the water is at about 12° centigrade; at the same time a temperature much below that which induces chill-coma in the Infusoria has no injurious effect on the animal's life, though it entirely prevents its growth. Indeed, observations have been made which seem to prove that the Limnæa may be quite frozen up without being killed. This mollusc grows at a very moderate rate; individuals brought up even under favourable circumstances take about three months to develope a shell twenty-four millimètres long, and they do not attain their full size under two years, although the whole life of the individual can scarcely exceed three or four years at the utmost. Assuming that a young Limnæa were placed in a lake or stream, of which the temperature constantly exceeds the minimum at which the snail can begin to grow, during only two months of the year, while it never perhaps reaches the high optimum, 25°, the mollusc will be unable to attain its due proportions during the first year, or to grow to its full size even during the second, and thus a dwarfed form will inevitably arise. This dwarfed

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form will still be able to reproduce and multiply itself; for the maturation of germinal matter—the ovum and sperm—takes place during the winter and early spring, at a time when the low temperature of the water hinders all growth, and the optimum of warmth for the sexual processes is much lower than that for growth. Thus a permanently diminutive race [33] might arise if the conditions of temperature above described remained constant for several successive years in the lake or stream where the young molluscs or the eggs have been deposited. Hence it has been supposed, and in many cases no doubt with justice, that the dwarfed races of animals which are found on high mountains or in the polar regions, where they must meet with the conditions of temperature just described, have originated directly from the low temperature hindering their growth. This assumption, as is quite evident, perfectly accords with my experiments on Limnæa; still it must not be forgotten that other influences might have precisely the same effect, such as insufficient food and other circumstances, which will be discussed in the next chapter.

Thus we have seen that a degree of cold nearly as low as the freezing-point of fresh water kills Infusoria, but not the Limnæa; also that their vital activity, as shown by the contraction of the pulsating vesicle, begins at 4° above zero, while assimilation, and with it the other organic functions, only begin in the Limnæa at 12° above zero, although the optimum of temperature which favours the highest vital activity and development is almost identical for both, viz. 25°. The enormous difference in the powers of resistance to a fall in temperature, possessed by different creatures, which is proved by these examples (and by many others which need not be particularly mentioned), shows that its influence is not *absolute*, *i.e.* cannot equally affect all the animals exposed to it; but that the extinction of certain animals under secular refrigeration in either hemisphere of the globe must have depended in part on the nature of the animal itself.

This reaction against the influence of cold is in the highest degree dissimilar in different species of the same family. A few special phenomena illustrating this, particularly those of hyber-

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nation or winter-sleep, and of resuscitation after being frozen up, must be briefly examined.

It is universally known that there are forms among the Vertebrata, as well as the Invertebrata, which are distinguished from all their congeners by the circumstance that they are lulled to sleep by the falling temperature at the beginning of winter; they sink into a state of rest of longer or shorter continuance, during which their active life, if not totally suspended, is reduced to a minimum. My two tame Prairie-dogs, Hans and Gretel, feel the effect of a falling temperature, when the thermometer is only down to 7°–10° centigrade; the Amphibia of our latitudes first perceive it when the temperature is very little above the freezing-point of water, while in Cuba they succumb at degrees lying between 7° and 24°; the common continental vineyard-snail, *Helix Pomatia*, does not throw off the calcareous lid which protects it during its four-months sleep till the temperature by day has reached about 10°–12° centigrade. In tropical countries, various animals, as snakes, lizards, &c., fall into a state of chill-coma, precisely resembling a winter sleep, at a temperature far above that at which the hybernating animals of northern latitudes [34] are still quite active—another proof of the truth of the statement that it is the departure from the optimum, not the absolute high or low temperature, that affects animals. In the Philippine Islands I have frequently found snakes under stones early in the morning, that were quite stiff, though the temperature of the soil under stones, or protected against radiation by the shade of forest trees, was never below 16°–18°. It may perhaps be here objected that, for this very reason, the winter-sleep of our animals cannot be directly compared to the chill-coma of those living between the tropics; but I think this objection ill-founded. Certainly the temperature in tropical countries never remains for any length of time, for days or even weeks, so low as to induce an unbroken or prolonged chill-coma during such periods. But it is obviously of small consequence whether the effects produced by the lowered temperature are of long or short continuance; even among our hybernating animals the duration of their sleep varies considerably, but the general

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identity of the influence exerted by a reduction of temperature, both in high latitudes and equatorial regions, is not to be disputed. This consists, as we have seen, in the fact that every reduction of temperature below the optimum, whether that optimum be high or low, so diminishes the vital energy of many, though not of all animals, that they gradually fall asleep, and remain in a condition resembling sleep as long as the low temperature, which induces that condition, lasts.

In general, warm-blooded animals seem to be protected against the effects of a reduced temperature by their power of keeping up, by combustion, the warmth indispensable to their existence. But they do not all escape its influence nevertheless. Everyone who has lived for any length of time between the tropics, and has observed the people there, knows that the natives become excessively sleepy under a sudden and great diminution of warmth; and that the most inveterate winter-sleepers belong to the warm-blooded mammals is equally well-known. It is in no way surprising to learn that a cold-blooded snail, mollusc, or frog becomes lethargic during the winter, because the warmth of their bodies always exactly or very nearly corresponds with that of the surrounding medium, air or water, and because they are not fitted by their internal structure to produce such warmth as is indispensable for the energetic vital action of their organs; hence they must gradually subside into sleep, *i.e.* a torpid condition of life, as soon as the temperature of the air or water falls below the point where their powers of assimilation begin. But we may well feel surprise at seeing that a warm-blooded animal, whose body is constantly maintained by internal processes at the high temperature of from 36° to 38°,[35] is nevertheless incapable of resisting the lowering and soporific influence of cold. With regard to this point a fact of the greatest importance has lately been discovered. We have learned from tolerably numerous observations that in several hybernating mammals, which have been examined with this view, the temperature of the body is very considerably lowered during their winter-sleep. The lowest temperature hitherto detected in such a creature is 2° centigrade in the Zizel, *Spermophilus citillus*, according to Horvath's researches. To this naturalist [36]

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we owe, too, the far more interesting observation, that the Zizel, when lying in its winter sleep, always has the same, or nearly the same, degree of warmth as the surrounding air. In one case the temperature of the room was 2° above zero, and a thermometer inserted in the rectum marked exactly the same degree; in another experiment the animal was sleeping in a room, at about 9° to 10°, for several days, and its body (in the rectum) was at 8·4°. This shows that during their winter sleep warm-blooded animals become truly cold-blooded: at any rate this is true of the Zizel, since its temperature corresponds with that of the surrounding atmosphere. Other facts proved by Horvath's elegant experiments, and of which the interest is too specially physiological for mention here, I have quoted in Note 36, for they appear to me to deserve to be more widely known than they have hitherto been.

A second point of more general interest is the great power of resistance to extreme cold manifested by many animals, and their power of enduring even to be frozen up without injury to their vital functions. In this respect the cold-blooded have certainly the advantage over the warm-blooded races. Man is compelled to supply his deficiency of natural protection against severe cold in the most various ways, or to borrow them of furred quadrupeds; a rabbit will infallibly die if the heat of its body is reduced to 15° centigrade. Thus this rodent, whose normal body-temperature is about 31° to 32°, needs only the comparatively insignificant reduction of sixteen degrees to put an end to its life; and it is to be assumed that, with the exception of the winter-sleepers, the same would be the case with all mammals. But it is different with the cold-blooded animals. Their body-temperature, as we have seen, is always exactly or nearly the same as that of the surrounding medium, and rises and falls with its variations.[37] But their powers of resisting a considerable amount of cold are nevertheless very various, and even the same individual, at different stages of its development, differs greatly in this respect. Frogs and toads can bear to be frozen up, or even endure a degree of cold approaching the freezing point, only when fully grown; many fishes, as the salmon, can do so, both as embryos in the egg

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and when fully grown; it is well known that salmon's eggs, with the embryo in them, are conveyed in ice even to America and Australia; other animals, again, can bear such cold only in the egg state. Many insects perish in the winter, while their eggs survive, and the embryo within the egg of many insects cannot be frozen even at an extremely low temperature. The so-called winter eggs of many of the lower crustaceans—*Daphnidæ* for instance—and the germs or statoblasts of Bryozoa, or of the fresh-water sponges, resist any degree of cold, while the fully grown individuals regularly perish in the autumn, apparently from cold. So far as I know, no explanation has yet been given, or even sought for in the right way, of the fact that the soft contents of so minute a body as the egg or germ of an invertebrate animal cannot be frozen so long as it remains enclosed in its firm but always extremely delicate capsule.

With regard to the capability manifested by many animals, or even certain separate organs, of enduring to be frozen up without having lost their vital powers in the smallest degree after they are thawed, many observations have been recorded, but hardly any, if any, thorough and complete series of experiments. The statements that have been made are often nothing short of astounding. Thus it has been said that frogs and toads do not die even when so completely frozen that their skin, muscles, and bones can be broken up into fragments. The extremely delicate marine Naked Mollusca are said, like many other Mollusca, to endure freezing in ice without injury, and excised portions, as the heart, muscles, or nerves, to undergo the same treatment without losing their functional powers. But, on the other side, Pouchet declares, on the ground of various experiments, that actual freezing infallibly kills separate members, and perfect individuals too; for according to him the corpuscles of the blood are in the first instance destroyed by freezing, and these dead elements act as a poison after the individual is thawed, killing the animals, or, as the case may be, the organs. This view, if not actually contradicted by Horvath's researches, is rendered improbable, to say the least; for from them we learn that a frog whose legs have been killed by freezing lives on all

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the same, and is not poisoned by the introduction into its circulation of the dead corpuscles from its frozen legs. From Pouchet's point of view it might be answered that the amount of poison supplied by the freezing of the legs was insufficient to do permanent injury to the frog after they were thawed. But the question is not one of any present moment.

At any rate, the results of Horvath's experiments, which agree with Pouchet's, as to the deadly effects of freezing, make the various observations as to the revival by thawing of frozen animals in the highest degree improbable. Horvath showed that a frog, or a portion of a frog, infallibly died when frozen in a temperature of the surrounding medium (water or quicksilver) of 5° or more below zero C.; whereas nerves, muscles, and hearts, after being reduced to a temperature of from 0° to 4° below zero C. or even actually frozen, are said to be capable of renewed activity when thawed again. From this we may infer that the essential part of muscular fibre or nerve-tissue, on which their functional activity depends, is not brought to its freezing-point even when reduced to a temperature of 5° centigrade. But we cannot extend this conclusion to whole animals, for we do not know whether other parts of the body, as, for instance, the blood or gland-cells, might not freeze at a still higher temperature and die in consequence, and then the whole animal would undoubtedly be killed. However, exact estimates of the internal heat of animals thus hard frozen are not at hand; it was concluded at once from their stiffness that they were frozen through and through, without the least consideration of the fact that the freezing-point of the different juices found in the body may vary greatly, and that consequently, even in apparently hard-frozen animals, those parts may not be actually frozen on whose properties their resuscitation by thawing essentially depends. Horvath's experiments ought to have been repeated, in a comprehensive way, on uninjured animals before a positive opinion could be formed on earlier observations.[38]

Meanwhile these as well as Horvath's experiments show that there are animals which can bear to be frozen up, and even to be in part actually frozen. From this a latitude in their power of resistance to variations of temperature is presumable, which

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must be of the greatest importance in considering the question as to how far secular variations in the distribution of temperature on the surface of the globe may have acted as a selective influence on the animals peopling it. For instance, the selection from species now living, which might possibly at some future time recur as the result of a considerable reduction in the temperature of our latitudes and the introduction of new species from high latitudes—the fauna of the ice period—might be accompanied by modifications in the structure of the individuals of such species as survived the change.

Now, so far as I know, no single investigation proves that the coarser main structure of the different organs of animals can be modified by changes of temperature. On the other hand, many modifications in the fur and colouring of mammals, and in the colouring of birds and insects, may with good reason be referred to the direct or indirect influence of a reduced temperature; as regards insects, indeed, this effect has been positively proved by experiment. (Another effect of a falling temperature, namely, its influence on the production of eggs, will be treated of later.)

It has been recently asserted, on the contrary, that the change of colour in winter, which occurs regularly in many mammals and birds, is a result not of cold, but of selection. I must confess that I do not understand how such a conclusion is arrived at. It is self-evident that selection *per se* cannot possibly modify colour, *i.e.* the pigment itself, in the smallest degree; the causes which result in a brown fur becoming white, more or less quickly, must undoubtedly be of a different character. It is well known that the whitening of the hair in man is usually a sign of advancing years, that sometimes it occurs in early life, and that this peculiarity is often hereditary, and that occasionally violent and sudden agitation of mind will cause it within a few hours; in all these cases the efficient causes are perfectly dissimilar. But of the nature of these causes we are wholly ignorant; and we may, though with caution and reserve, express the view that the fall of temperature at the beginning of autumn may somehow produce an effect, direct or indirect, on the pigments situated in the skin.

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On the other hand, it is difficult to understand how a race of brown animals can be gradually transformed by selection into a variety which always turns snow-white in winter. Granting that a brown weasel could, by any external or internal cause, be changed during the winter into a brown and white spotted one, this weasel would not have the smallest advantage over the brown one in consequence of the white mixture in its fur, for it would be quite as conspicuous as a plain brown one in the pure white of the snow, perhaps even more so. That a white variety should arise from a gradual increase of the white patches in the piebald fur is not to be thought of. It might indeed be possible that a selection should be effected, if a pure white variety were at once and from the first produced from the animals which first exhibited this modification of their summer colouring, since these, like the nearly white ones, would in fact enjoy an essential advantage over the brown or spotted ones. But, even then, selection would not have produced this pure white winter colouring by the cumulation of small and useful variations, but have chosen between the two varieties offered, the white and the brown; and the question as to the origin of the winter colouring is still unanswered. The same arguments hold equally good for all pure white varieties, whether in arctic regions or on the ice and snow of high peaks in mountain chains; these, like all other species that turn white in winter—it would be superfluous to enumerate them here [39]—cannot have preserved their winter colouring by means of selection; whereas, no doubt, after other causes, unknown to us, had in the first instance given rise to a constantly white variety, or to one white in winter and brown in summer, this may have been secured by the rapid extirpation of the less well-protected brown or spotted varieties. It is thus that Wallace accounts for the occurrence of white species in northern regions, but he does not even refer to the question as to how the white hue originated.

The nature of these causes is in fact unknown; it was probably an error to assume that in all the above-mentioned cases this whiteness, *i.e.* the absence of the pigment, was the direct effect of the winter cold, or of the low temperature of the polar

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regions or of the eternal snow-fields of high mountain peaks. In one single case only can we assert with certainty that the winter colouring of an animal may be referred to the direct influence of the reduced temperature in autumn. Professor Weismann in Freiburg, to whom we are indebted already for many facts established by his elegant experiments, has proved that two varieties of butterfly, long regarded by entomologists as distinct species, are in fact only the summer and winter forms of the same species of Vanessa (*Vanessa prorsa-levana*), for he succeeded in rearing the winter variety (*Vanessa levana*) in the summer season, and from a summer brood, by keeping the air in which the caterpillars and pupæ lived at an artificially lowered and regular temperature.[40] It is much to be wished that zoologists would more frequently carry out

FIG. 29.—*Desoria glacialis*, the Glacier Flea.

similar experiments; for if this were done, I have no doubt that a far more extensive influence of cold on animals would soon be recognised, and its limits more accurately defined than is at present possible.

II. The influence of a rising temperature on animal life.—Variations in temperature below the freezing-point of the fluids contained in the body can obviously have no effect on those animals, or on their peculiarities, which either die when the cold reaches that point, or whose vitality becomes latent. It will matter little to a perfectly frozen frog whether it was frozen at 5° below zero or at 10° or 12° above. It is not until the water surrounding the creature, and the fluids contained in its tissues, recover their fluidity under a thaw, that any further rise of temperature can affect its vital activities. For although many animals can live on snow and ice, or even in ice—as the

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glacier flea (fig. 29), *Degeeria nivalis*, two species of *Sminthurus*, *Chionea araneoides*, &c.—their internal temperature is not that of the ice; nay, most of these creatures belong to the warm-blooded races, who themselves can supply the deficient warmth. Besides, the temperature of the air at the surface of the ice or snow is by no means always below the freezing-point; on the contrary, often considerably above it. The fact that animals live on or in the ice must not be taken as proving that an active animal life is generally possible at temperatures below zero, or that a rise in the temperature of the air or water from $-10°$ to $-5°$ can be of any importance to animal life. A rise of temperature above the freezing-point of the water and of the juices of the body must, on the contrary, have much effect on the animals; but, as we have seen, it has by no means the same effect on all the animals that live together in one spot and exposed to the same rise in temperature.

The effect of a rising temperature on animals depends of course on their nature; as this differs, so will they be differently affected. This is familiar to all, and easily observed. Some animals rouse from their winter sleep earlier than others; some at a low temperature remain rigid in morning torpor, while others, roused to sexual activity, display their charms, and are already busy, laying their eggs or bringing forth their living young. In short, from the very freezing-point, a rising temperature begins to exert its stimulating influence on the vital functions of every living thing up to the point where these functions are at the highest possible stress under the optimum of temperature, which, as is proved by the above-mentioned facts, is different for every animal. If the heat rises above this optimum, the effects are reversed; functional activity is more and more reduced, till at last a sleep-like condition or heat-coma precedes death, which ensues under too great heat.

The optimum of temperature varies not only according to the species, but in every individual, nay, in every organ of every individual. The best, or at any rate the best known, example of this is offered by the Infusoria. Rossbach, in the work already referred to, showed that the rhythmical contractions of the contractile vesicle always grew more rapid under a rising

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temperature until they reached the maximum of rapidity, which varies in different species, at the temperature of 30° centigrade. If the heat increased beyond that point, the rapidity of the contractions diminished, while at the same time that of the ciliary movements increased; if, finally, a temperature of 35° was attained, a striking difference was seen in the reaction of two kinds of cilia; those which effect the rotatory movement move without being in any way affected by the animal's will, while the others, by which the creature is enabled to move backwards or forwards, depend entirely on its will. The rapidity of both kinds of motion increases equally so long as the warmth is rising up to 35°, but after that the backward or forward motion of the animal ceases to be under the control of its will, and a peculiar combination of aimless direct and rotatory motions is the result. When the heat has risen to 40°, the direct motion which became involuntary at 35° ceases entirely, while rotation continues with undiminished vigour, till at last between 42° and 45° heat-coma supervenes and death ensues. We see by this that even two so closely allied functions as contractility and ciliary motion, or even two very slightly different kinds of cilia—those that work voluntarily and involuntarily—are influenced in widely different ways by the same increase of temperature, exactly as individual animals react differently under a rising temperature. Hence an increase of temperature, in any district, resulting from secular variation, or an alteration in the distribution of heat as to the seasons, must exert widely different influences on animals previously living together; and the view so frequently expressed in the statement that animals may be classed as tropical, sub-tropical, temperate, and so forth—as if all the animals living together in the same place must be equally well adapted to the climate of it, and as if they must all react in the same way under any variations in temperature—is evidently devoid of any solid foundation.

We will now examine a few particular instances, to illustrate more exactly what has been said by some extreme examples.

We know that the optimum of temperature is not the same for all animals,[41] so we shall not be surprised to see that certain species can live in a temperature which to others is

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promptly fatal. Animals of the North Sea, when exposed to a temperature of 30° under the direct rays of the sun, die, it would seem, at once, and invariably, while this appears to be the optimum of warmth for the *Branchipus stagnalis*, living in our pools. Animals living within the tropics are generally exposed to a much higher and more equable temperature than our northern or boreal forms, and few species can long survive a transfer from one region to the other. I shall presently return to this subject. It certainly appears surprising, though it is an indisputable fact, that certain animals and even plants are capable of enduring a higher temperature [42] than is generally fatal, as it would seem, to protoplasm, which is the fundamental element of all organic life. It is known that animal protoplasm usually coagulates and dies at 40° centigrade, and always at 50°, and this agrees with what is known of vegetable protoplasm. Hence we should feel inclined to conclude that animals could not exist in spots—as, for instance, in many hot springs—where the temperature exceeds the maximum limit in which protoplasm can live. But this assumption is in contradiction to ascertained facts. It is superfluous to give these in detail; it will suffice to state that animals of tolerably high grade, as Crustacea, the larvæ of insects, &c., live in springs having a temperature of 50°–60° or even more. In view of the numerous data on this subject, and the trustworthiness of most of the observers, we are not justified in doubting the facts, although the physiological puzzle which they offer cannot at present be solved—indeed, no attempt has ever been made to solve it. We might have recourse to the supposition that the capability of many animals for living and multiplying in such heat must result from a capability in their protoplasm for resisting the injurious effects of a temperature of 50° centigrade and more. But this would prove far greater powers of adaptation in animal protoplasm than have yet been considered possible.

It might perhaps seem plausible to many readers to assume that immunity from the injurious effects of too great heat bore some analogy to immunity from injury from too great cold. But such a parallel is not admissible from a closer and more exact point of view. Every fall of temperature below

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the optimum diminishes the vital energy of the creature more and more, till at last, at the minimum, life becomes latent; in this condition the animal can live for a long time without danger, since the consumption of organic nutritious matter is at its minimum, or, as it would seem in eggs which survive the winter, almost entirely suspended during long periods. If, on the other hand, the temperature rises above the optimum, the vital energies are more and more increased, often accompanied, no doubt, by phenomena which seem to indicate a certain deterioration in them; but a condition of latent vitality never supervenes; on the contrary, death always follows as the result of a too rapid consumption of the organic matter of the body. Thus the power possessed by many animals, both warm- and cold-blooded, of enduring without injury a higher temperature than that which kills protoplasm, remains as yet unexplained even by the parallel above suggested, and the solution of the problem would undoubtedly be of the highest interest.

However, the experiments and observations that have been made suffice at any rate to prove that the optimum of temperature differs for individuals, and even for the different organs of one individual. We have seen that the control which an Infusorial has over its progressive motion is lost at a degree of heat above which the actual movement itself continues to increase in rapidity, and we saw too that the rotatory motion continues to be accelerated up to the very point at which death ensues, while progressive motion ceases at a much lower degree. Hence we need not be surprised to see that a rising temperature sometimes produces phenomena which apparently resemble those produced by increased cold. Everyone knows that Europeans in tropical countries, or even in a hot summer's day in our own latitudes, become very sleepy, exactly as natives of the tropics do under the influence of a cold climate. In these cases we are justified in assuming that the too great heat deprives us of the stimulus which usually keeps us awake during the daytime. An attempt has been made to refer the 'summer sleep'[43] of many animals in hot countries, as analogous to 'winter sleep,' to a long continuance of such soporific influences; but this is certainly not correct; in all these cases it is most probable that the

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drought which prevails during the hot season is the direct cause of it, as will be more fully shown in a future chapter.

One more effect of rising temperature must here be mentioned as influencing one particular function, on whose normal action the existence of every species primarily depends—the multiplication of individuals, or reproduction, either by eggs, or by fission and budding. Every modification of this function must exert a direct and considerable influence, either selective or transforming, on every separate species. If, for instance, we suppose that the animal temperature in any country were to be so modified that the optimum temperature for the production of eggs did not occur at the proper season nor last a sufficiently long time, all the animals affected by the change would be infallibly exterminated, and the fauna would be utterly transformed at a single blow. The influence of a rising temperature on the eggs already laid, and about to develope after their winter rest, would be almost equally important, as affecting the composition of the fauna of a country. Before going into particulars, it will perhaps be well once more to remind the reader that by the words 'rising temperature' I mean, not an increase of heat from a fixed minimum to a certain uniform maximum, but a rise from any degree above zero to any other, the optimum—two points which, as we have seen, have no direct reference to the degree of temperature, but only to the mode in which they may affect animals.

It seems to me superfluous to adduce any special instances in support of the well-known statement that egg-formation undoubtedly begins—in other words, the sexual powers attain maturity—under a rising temperature. No experiments, however, have hitherto proved how this effect is produced by heat, whether heat alone can have that effect, or whether it requires other concurrent circumstances; nor at what degree of rising temperature the result is produced in different animals. Several observations accidentally made[44] appear to be most happily explained by this hypothesis of the effect of warmth, but no attempt has been made, on any comprehensive method at any rate, to supply an exact answer to the questions to which those very observations first gave rise. Thus, for instance, and to go

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no further, the fact that many animals lay different eggs in the summer from those they lay in the autumn may be directly referred to the difference of temperature at the two seasons, and they are accordingly known as summer eggs and winter eggs. But the formation of eggs certainly does not only depend on warmth, but also on food, both as to quantity and quality, as well as on the chemical conditions of the surrounding medium, the moisture of the air, and other conditions; so that it must not be assumed out of hand and as certain that this classification (according to the seasons) of the two forms of eggs, which occur among Crustacea, Insects, Rotatoria, and others, is invariably appropriate; on the contrary, it needs direct experimental

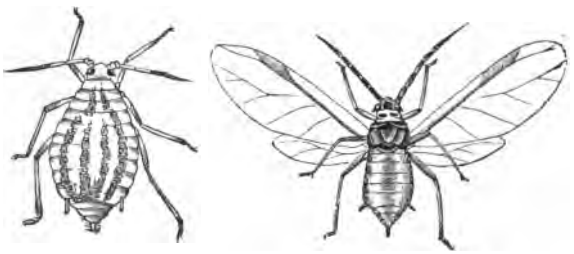

FIG. 30.—*Aphis Beccabungæ*, a Plant-Louse. To the left the wingless, and to the right the winged, form of the female.

proof in each separate case, and this, as I have said, has not hitherto been obtained on any comprehensive method.

In a few cases only have we experimental evidence that the formation of a particular form of eggs (and mode of reproduction) directly results from variations in temperature. Thus, for instance, we know that the Aphis (fig. 30), a family of the Hemiptera well known as the Plant-Louse, sometimes in a favourable summer produces as many as fourteen generations by *parthenogenesis*, as the eggs then produced do not need fertilisation by the male. At the beginning of the cold season males first make their appearance, and the eggs fertilised by them live through the winter, being known as winter eggs, till the next spring, when the rising temperature developes and hatches the embryo. Now, if the summer Aphides that multiply by par-

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thenogenesis were not exposed to the effect of cold, but kept in a constant summer heat, and at the same time supplied with suitable food, no males would occur, and the young would be uninterruptedly produced by the parthenogenetic mode. In fact Réaumur did succeed in this way in producing artificially above fifty parthenogenetic generations in the course of three or four years, all descended from one mother. The converse experiment has never, so far as I know, been made—namely, whether it would be possible to produce males in the spring by

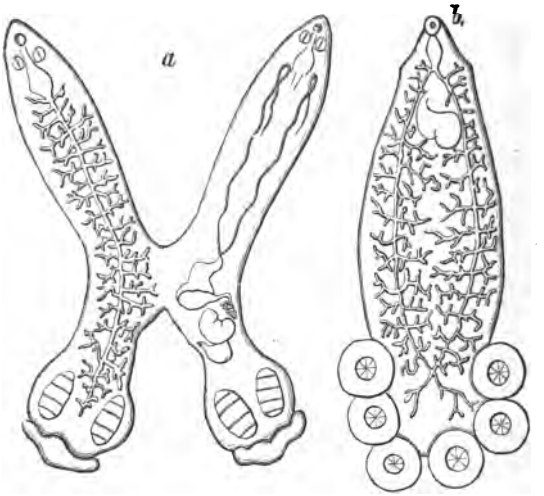

FIG. 31.—*a*, *Diplozoon paradoxum*, from the gill of a fresh-water fish ; *b*, *Polystomum integerrimum*, from the bladder of a frog.

artificially lowering the temperature, although they do not properly appear till later in the year, and thus to diminish the normal number of successive parthenogenetic generations in a summer. It is highly probable that it might succeed.

The facts lately communicated by Zeller are no less interesting. He found that certain parasites, in precise opposition to the Aphides we have been speaking of, *Diplozoon paradoxum* and *Polystomum integerrimum* (fig. 31), produce true eggs in the summer only, which must be fertilised before they can

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develope, and that the formation of eggs ceases entirely at the approach of the cold season. But the production of eggs can be artificially prolonged throughout the winter if the fishes in whose gills the Diplozoon lives are kept in an aquarium in a room where the temperature is kept up to summer heat. It must be assumed that in this case, as in that of the Aphides, all the other conditions of existence, and the supply of food in particular, were kept up to the optimum, for the effect of bad food would apparently have made the results of all the experiments in question very doubtful. Unfortunately we learn nothing from either Réaumur or Zeller on this point, nor are the exact limits of temperature given, nor any thermal curves by which we may gain some idea of how the production of eggs is dependent on the variation of the temperature between two fixed limits. From the fact that in the brooks and streams, at the bottom of which the fish live to which the parasites are attached, the temperature is considerably lower than that of the atmosphere in summer, we may certainly infer that these curves of temperature are quite dissimilar for the Aphides and the Diplozoa, and that the optimum of temperature for the production of eggs fit for fertilisation is probably also widely different. And thus, again, a selective influence might arise from any general change of temperature that might take place, and affect the animals of the region where it occurred, since the existence of a species largely depends on the normal succession of generations.

We saw a little way back (p. 108) that the growth of an animal is indirectly affected even by the temperature of the surrounding medium, since the assimilation of the amount and kind of food which is indispensable for growth can only be carried on to full advantage under a very different optimum of temperature for different animals. In the second place, we are also justified in supposing that this optimum for the animal's growth is not identical with that for the production of eggs.[45] If now we recollect that the maturation of the eggs usually requires but a short time,[46] while the growth of even very small animals often takes a long time—in Polystomum, for instance, several years—it plainly follows that sexual maturity does not,

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as is often assumed, necessarily indicate the completion of individual growth. They may no doubt coincide, but they need not; and instead of being surprised, as is frequently the case, at finding that larvæ, *i.e.* animals not yet fully grown, are sexually mature—*e.g.* Salamandra, Siredon, Blatta, and others—we ought rather to wonder that it is only quite recently that such cases have been investigated and considered worthy of record. An example of this kind, recently observed by me, is offered by the land-snails of the Mediterranean province. It is known that on high mountains or in high latitudes land-snails are frequently hindered by the low temperature from assimilating within a given time as much nourishment as others of the same species living on the plain or in a warmer climate, so that they never attain the same size, though they are capable of reproduction. In this case it would be possible that the first sexual maturity and the last stage of growth might coincide, although the mature animal was of a small size. It is quite otherwise with the snails of the warm Mediterranean region. These, as I know from my own observations, are brought to sexual maturity by the time they are six months old by the intense heat combined with the sufficient moisture of the spring, though they are not fully grown; after a summer's rest of three months, occasioned by the drought, a second period of egg deposition occurs at the beginning of winter, although the full size of the animal, as indicated by the completion of the margin of the mouth of the shell, is not attained till the second period of sexual activity. Thus species of the same genera, perhaps even the very same species, in our damp and cold climate, do not produce a new generation till they are fully grown, while in the dry warm region of the Mediterranean they have produced two generations before they are fully grown. This is probably the true explanation of what are known in the terminology of the zoologist as Larva-forms,[47] a name given to all animals which possess the characters of the larvæ of other species and are nevertheless capable of sexual reproduction. Such larva-forms occur in almost every group, in Vertebrata, Mollusca, Ascidians, Worms, &c. A very striking example occurs, among creatures of such high physiological development

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as insects, in the well-known walking-stick insects, allies of the grasshoppers (fig. 32), which resemble a more or less dried-up twig or shoot. Many of these species are wingless, so that they bear a wonderful resemblance to the larvæ of other, winged forms. If then we assume that the wingless forms are the progenitors of winged forms, the origin of the winged forms may be very well explained by the further assumption that the optimum temperature necessary for maturing the eggs may have been raised so much as to afford more time for assimila-

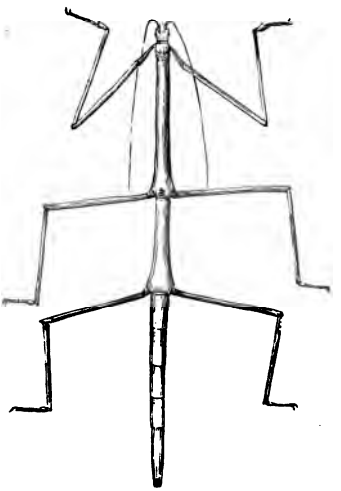

FIG. 32.—*Phasma* sp., a wingless orthopterous insect.

tion and growth, and consequently for more extensive modifications of structure. If, on the other hand, we regard the wingless species as the later form and derived from the winged species, their origin may be easily explained by assuming that the optimum of temperature for the maturing of the eggs was lowered, while the optimum for growth remained the same. For we know that in many cases, particularly among insects, the life of the individual ends as soon as the eggs are mature and deposited, and that the performance of this function seems

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to absorb their whole vital energy; thus an animal which was forced by such external conditions as we have been supposing to lay its eggs while still in the larva stage must always, if it dies soon after from exhaustion, produce only such progeny as are sexually mature in the larva-form so long as the conditions remain the same—in this instance, namely, a low optimum of temperature for the maturation of the eggs.

We will here interrupt this chain of hypotheses, since they are introduced merely to explain the possible origin of such an apparently paradoxical sexual larva-form.

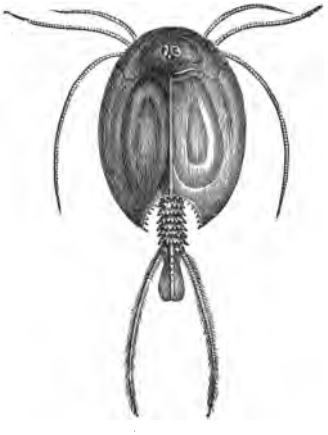

FIG. 33.—*Apus.*

We must, however, briefly touch on another circumstance which plainly demonstrates the direct influence which may be exercised by variations of temperature on the growth and development of individuals.

The general effect of a rise of temperature on the development of the embryo and young animal is well known. We know that a hen's egg requires for its quickest normal development a warmth kept as constantly as possible at 40° centigrade; at a lower temperature the development will be delayed, while at the ordinary temperature of a sitting-room it ceases altogether. The eggs of certain Crustacea, on the other hand, as *Apus* (*Lepidurus*;

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fig. 33) and *Branchipus*, can endure much greater variations and develope equally well at any point between zero and 30°. The difference between the extremes of temperature which, on the whole, favour the development of these eurythermal eggs (having, that is, a wide range of temperature) is apparently even much greater, although even with them the rapidity of their development depends on a rapid rise of temperature to a tolerably high degree.[48] Thus I myself have observed the larvæ of *Branchipus* and *Apus*, known as *Nauplius*, hatched out in less than twenty-four hours at a temperature of 30° cent., but at 16°–20° they required some weeks. The same effects of variation of temperature were observed by Higginbottom in the larvæ of frogs; he found that at a temperature of 51° F. (=10·5° cent.) they hatched in twenty-one days, but at 60° F. (=15·5° cent.) they hatched in ten days. Hence a rise in temperature of only 9° F. (=5° cent.) doubled the rapidity of development of these embryos. The difference is still more conspicuous if we compare the time required in the two cases for the whole process of development from the time the egg was laid till the metamorphosis was complete. At the lower temperature of 51° F. 235 days were needed, at the higher, 60° F., only seventy-three days. Many other examples might be added to these, all proving the same effect of a rising temperature; but unfortunately, so far as I know, none give any exactly determined thermal curve for particular species, and all that is clearly shown by these observations, often merely incidentally made, is the fact that the eggs of different, very closely related species behave in a totally dissimilar manner. An increase of temperature in a district, occasioned by no matter what cosmical causes, may thus affect some animals particularly favourably, while it injures others, since for the former it may merely raise it to the optimum, while for the latter it exceeds the maximum they can on the whole endure. In this way, by acting on the sexual activity and the rapidity of growth in the young animals and in the embryo, a transforming influence may be closely connected with the selective influence exerted upon the various species generally. It would certainly be an interesting and valuable task to investigate this point with accuracy.

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III. The influence of constant temperatures, but at different degrees.—We have seen that a fall below the optimum of temperature or a rise above it is more or less injurious to the animal, according as it ranges more or less near to the fatal maximum or minimum. If there were a spot where the heat was absolutely invariable, and if the degree of heat there exactly corresponded to the optimum for the animal, if also by this means the injurious influence of variation were excluded, absolutely favourable conditions for the life and growth of the creature would prevail, so far as warmth was concerned. It is evident, however, that very few animals live in such a perennially equable climate; none in fact but the parasites living inside warm-blooded animals and the creatures at the bottom of deep seas and lakes enjoy such an advantage. All others are exposed more or less to the effects of great periodical variations. Among these, however, those are evidently the most favoured which are exposed to the smallest deviations above or below the optimum. Hence a climate where the mean annual temperature differs in only a trifling degree from the winter or summer mean temperature, or from the extremes of heat and cold, will be the most favourable; such an equable climate may occur in high latitudes as well as between the tropics, since its existence depends less on latitude than on the configuration of the land, the vicinity of the sea, and the predominant direction of winds and currents. For example, the eastern half of both the old and new continents are distinguished from the western by having what is called an 'extreme' climate, in which the extremes of heat and cold lie far asunder, while England, and still more Ireland, are characterised by an extraordinarily equable climate as compared with many more southerly parts of the continent, which, like the countries of south-eastern Europe, have a continental, *i.e.* an 'extreme,' climate, with great heat in the summer and severe cold in the winter.

Before entering on a discussion of the question as to how far the theoretically assumed advantage of an equable climate is practically real, I must anticipate one view which might otherwise be regarded as the inevitable consequence of the foregoing statement. It might seem as though it stood in trenchant

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antagonism to another which is frequently repeated and supported by numerous examples, namely, this: That animal life, and more particularly the culture of the human race, can only attain their highest development in cold climates, although as a rule, not without exceptions, these manifest greater variations between the two extremes of temperature than tropical or subtropical regions. The high degree of culture that obtains among European nations is only attainable, so it is said, in the region of the north temperate zone. No contradictory evidence, it is true, is forthcoming. It might indeed be asked why humanity has not attained to so high a degree of culture, nor the animal world even reached such perfect development, in those parts of the southern hemisphere which have a cold or excessive climate, as they have done in Europe. But quite apart from this objection, which is certainly open to discussion, the opportunity afforded by favourable circumstances to some particular species of developing every individual to an average degree of perfection and fitness on the one hand, and the value which greater contrasts in temperature—that is to say, actually unfavourable conditions of existence—may have in the modification and progressive development of a species still capable of such modification, are by no means identical. For it is self-evident that the necessity for enduring abrupt alternations of heat and cold can only be met by greater powers of resistance in individuals and by enlarged powers of adaptation; hence, in extreme climates, the selection which will necessarily be effected by the violent contrasts of temperature, must, by eliminating the weaker individuals, improve the race; while in equable climates, where this mode of selection is absent, the weaker individuals (weaker only in this one point) have as good a prospect as the stronger ones of a long life and of transmitting their characters. The two propositions, indeed, do not contradict each other, but on the contrary complete each other. A species whose individuals are at an end of their capability for undergoing modification will succeed best in an equable climate, since there every individual, without exception, will find an equally favourable opportunity for reproduction—supposing of course that no other selective agency is at work. But so long as a

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species is capable of modification, the greatest alternations in the conditions of existence will offer the most favourable opportunities for its transformation and improvement—thus, in the case in question, the utmost variations of temperature—since it is in this way that the most stringent selection is effected between the weak and the strong.

Among the numerous instances which here offer themselves for discussion, want of room compels me to select only a few of the most significant. One of the first in importance seems to me to be a case of which the full value was first recognised by Möbius, who also, and apparently with perfect accuracy, referred it to its efficient cause. He mentions [49] the fact that the same species of Mollusc, living on the coast of Greenland or in the Baltic Sea, was in the former instance very large, and in the latter small and thin-shelled; and he attempted to explain this difference by saying that the animals in the Baltic are exposed to very considerable variations in temperature between the summer and winter, and are sometimes even frozen up, while on the coast of Greenland they live in a temperature which, though of course low, varies but little from winter to summer. Hence they are enabled to carry on the assimilation of food at an equable rate all the year round, never being disturbed by too great a heat in summer or too severe a cold in winter, while those in the Baltic are every year exposed to the liability of being checked in their growth by a too high or too low temperature in constant alternation. Although the mean temperature of the Baltic is higher than that of the sea off Greenland, the constant low temperature, *i.e.* the equable climate, of the latter is infinitely more favourable to the growth of the animal than the higher mean temperature with constant variations of the Baltic.

The numerous cases of successful acclimatisation lead us to the same conclusion. So far as I know, the old system is now given up in every zoological garden, by which foreign animals were kept in houses or cages in which an attempt was made to keep up by artificial means such a climate as they were used to; a contrary plan is now introduced, by which the animals are accustomed as quickly and thoroughly as possible to the

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new climate and to an open-air life. Unfortunately it would be impossible, without an enormous amount of labour, to arrive at any general views as to the results obtained in all the different zoological gardens in Europe; but in general it seems beyond a doubt that these attempts have succeeded best where the animals were introduced to an equable climate, and least well in gardens in the eastern region, where the climate is essentially continental, *i.e.* extreme. The first statement, that the acclimatisation of even tropical animals may be successful in an equable climate, though much colder than that of which they are natives, has found a striking and in every way interesting proof. Mr. Charles Buxton,[50] a rich member of Parliament, made such an experiment on a vast scale. He kept during many years numerous individuals of eleven species of cockatoos and tropical parrots in a large glass house; he then all at once gave them their liberty, putting them out into a wood contiguous to his garden. Being accustomed to be fed at fixed hours in the glass house, they came regularly down into the courtyard; but though the house was open to them, with nesting boxes to breed or to winter in, they built nests of their own accord in hollow trunks, and bred and wintered there, and, though exposed to a temperature of 7° below zero centigrade, not one died. It must have been a beautiful sight when the flock of gaudy parrots came crowding down in midwinter to pick up their food on the snow-covered courtyard. Many species were propagated, and even a hybrid race was produced between a scarlet and a white cockatoo; the young of these were distinguished from their parents by a fine orange-coloured tuft on the head. In view of the well-known effects of hybridisation, it would of course be absurd to ascribe this result to the effect on the parents of a climate to which they were not accustomed; but it proves that animals which we are wont to regard as incapable of living in freedom in our climate, because they are tropical species, are not only able to do so, but can propagate their kind and effect a voluntary cross-breeding which, if it were attempted artificially, would probably not succeed even in their native country. However, the climate of England is very equable in temperature, and it is more than

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doubtful whether such an experiment would succeed in central Germany, for instance, or in the east of Europe.

Everyone knows that in European countries animal life exhibits a very marked periodicity. The greater number of our birds quit us in the winter; many Mammals, Insects, Molluscs, &c., hybernate in a condition resembling winter sleep; others die off altogether, as Sponges, Bryozoa, many Crustaceans, Insects, &c., after laying eggs which survive the winter and are developed in the spring. The creatures that live in streams and lakes, nay, even on the sea-shore, breed only once, or at most twice, in the year, some in the spring or summer, others late in the autumn or at the beginning of winter, as the salmon. This periodicity depends apparently on the direct effects of the severe extremes of summer and winter temperature to which animals are exposed when living in temperate continental climates. This conclusion is easily proved by the following considerations.

Every individual requires a certain duration of life to achieve its individual development from the egg to sexual maturity and full growth; the length of time requisite for this is very various, and, above all, bears no proportion to the size attained. Animals grow at very different rates; the minute *Polystomum* which is parasitic in the bladder of the frog (fig 31) requires, according to Zeller's latest investigations, about five years to attain its full growth, while the *Apus* (fig. 33), a Crustacean of much larger dimensions, and *Branchipus* reach their full size in a few weeks of a warm summer. This length of time, which we may generally designate as the period of individual growth, is not alike even for all the individuals of the same species; on the contrary, it depends on the co-operation of so many different factors, that it must necessarily vary considerably. Now, if from any cause the period of individual growth, say of the salmon, became changed in consequence of the slower development of the embryo in the egg or of the young larva, most or all of the young salmon thus affected would die in our climate, because the greater heat of spring is injurious to them at that stage; or, on the other hand, an animal which is usually hatched during the summer, so as to attain by the autumn such a size as may enable it to resist the cold of the

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winter, would probably die in the winter if its growth during the summer were checked by any cause. Thus a climate that varies between two remote extremes of temperature must necessarily give rise to a sharply defined periodicity, by excluding those forms which have by nature a somewhat prolonged period of individual growth, since these, as the conditions requisite for their development are not fully satisfied, must have to contend with the temperature which checks their growth.

The opposite state of things must prevail in equable, and above all in tropical climates, where the variations in temperature are reduced to a minimum; here the periodicity of animal life must be to a great extent obliterated, at any rate in so far as it depends on temperature. For every individual of a species, even if its period of individual growth is longer or shorter than the average of the species, can live and multiply if it is never exposed to an absolutely fatal degree of heat; according to the laws of inheritance, its progeny will probably have a tendency to develope more or less slowly, and so by degrees one individual, whose period of individual development is short, may produce, let us say, six generations in a year, while another of the same species, but of slower growth, may produce only four. In this way all periodicity, as regards summer and winter, must be entirely lost, and at last fully grown individuals and young ones, larvæ and freshly laid eggs will all be found together at every season and in every month of the year. Such cases, in fact, are not uncommon, although they have been but little heeded hitherto. Nothing in the Philippine Islands struck me so much as to observe that there all true periodicity had disappeared even from insects, land molluscs, and other land animals; I could at all times find eggs, larvæ, and propagating individuals, in winter as well as in summer. It is true that the drought occasions a certain periodicity, which is chiefly perceptible by the reduced number of individuals in the dry months and the greater number in the wet ones; it would seem that a much smaller number of eggs are hatched under great drought than when the air is very moist. Even in January, the coldest and driest month, I found land snails which require much moisture, and at every stage of their development, but only in shady spots, in woods, or by the

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banks of streams. But what was far more striking in these islands was the total absence of all periodicity in the life of the sea animals, particularly the Invertebrata; among these I could not detect a single species of which I could not at all seasons find fully grown specimens, young ones, and freshly deposited eggs. Even in cold seas periodicity is far more often eliminated than is commonly supposed. Nordmann tells us that he has found the eggs of a sea mollusc (*Tergipes*) at all seasons, even in midwinter, when the temperature of the water was only at a few degrees above freezing-point; Möbius [51] states that eggs of Mollusca and Worms were found at all seasons of the year in the Baltic, and I hope that Dohrn's zoological station at Naples may ere long furnish us with a long list of species which may be observed the whole year round in all the stages at once of growth, larvæ, and eggs. So far as I can judge from my own observations, which of course are by no means conclusive, the Mollusca manifest the least periodicity in their reproductive powers.

The influence of an equable temperature on the inhabitants of the sea is displayed, too, in another manner. It is known that in our northern seas the daily variations of temperature on the shore, or even at some depth, are not inconsiderable, while in tropical seas the variation at the surface even between winter and summer heat is not nearly so great—at the Philippines, for instance, not more than 2° centigrade; so small a variation, as has been shown by Meyer and Möbius in a remarkable work,[52] occurs only at a great depth in northern seas. It is to this apparently that we must refer the fact that many genera of sea-creatures which are known as boreal forms live in the north at great depths, while in tropical seas they live very near the surface.[53] In my monograph on the Holothuridæ I have shown that a great number of genera which we had been accustomed to regard as typically boreal were found also in the Philippine seas, and lived there at a moderate depth, while in the northern seas they were found only at very considerable depths. The same seems to be the case with regard to many animal forms which are now found at the bottom of the Atlantic, and which may be regarded as survivors from a long past geological period;

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an inconceivable variety of these forms was brought to light by the 'Challenger' expedition. A woodcut is here given of one of the most beautiful of these species, the *Euplectella*, which belongs to the group of Sponges (fig. 34). Although the results of the 'Challenger' expedition have not yet been fully published, so that it is impossible to give a complete list of the various deep-sea forms and their distribution vertically in depth, it seems to be tolerably certain that they have a much wider vertical distribution in tropical seas than in northern oceans; in the north, for instance, no Euplectella nor any allied form of sponge—six-rayed Siliceous Sponges—has been found in a less depth than 300 fathoms, while in the Indian Ocean they are common in 100 fathoms or less. Thus the higher temperature of the water to which these cold-water animals[54] are exposed in tropical

FIG. 34.—*Euplectella Aspergillum*, a siliceous sponge of a group which consists mostly of fossil forms.

seas is in no way prejudicial to their existence; and this can only result from the fact that these animals are better able to bear a difference of temperature, so long as it remains equable, than variations between two extremes lying far apart, and to which they are more or less suddenly exposed.

Here, in conclusion, we must briefly discuss an application of the foregoing statements and arguments to Palæontology.

It is generally assumed that we are justified in attributing to extinct animals a mode of life analogous to that of the nearest related surviving forms. But, in the first place, it is often extremely difficult to decide what may have been the nature of the affinities between extinct and living animals, and it cannot be disputed that, in instituting such comparisons, we are often obliged to judge by characters which in no way warrant our

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forming any decisive conclusion. For instance, far too much value has been attributed in this way to the in-operculated Terrestrial Mollusca (*Pulmonifera*); for, in my opinion, it is absolutely impossible to form any opinion as to the affinities of extinct animals by comparing their shells, which are all that remains of them, since recent investigations as to living Pulmonifera show that very often species of the same genera have quite dissimilar shells, while, on the other hand, the shells of many species belonging to quite distinct genera, or even to different families, are so much alike, that until quite recently they have been considered as species of the same genera. I shall enter more minutely into this subject somewhat later on.

Even if we were prepared or obliged to admit that the fossil remains in every instance allowed us to determine the affinities of the species to living animals with absolute certainty—and not in the case of Vertebrata only, but in the Invertebrata also —still we might assert, and defend the position with success, that the extinct species need by no means necessarily have lived under the same climatic conditions as those forms which are now regarded as their nearest living allies. For we have seen that animals which in separate spots are stenothermal (enduring but a small range of temperature) are able to exist in very dissimilar temperatures when the whole extent of their distribution is taken into consideration; thus *Euplectella* and *Semperella* live in a constant warmth of about 15° in the Philippine seas, while their nearest congeners can thrive in other localities in so low a temperature as 1° above zero, which is the temperature of great depths in the Atlantic. We have seen, moreover, that animals, as parrots, which live almost exclusively in the tropics under a mean annual temperature of 26° to 28° with a variation of from 6° to 8° at most, can nevertheless subsist in the open air in England, multiply, and even produce new 'sports' or varieties, although living in a mean annual temperature of only 12° to 13°, with a variation between the extremes of as much as 17°. Thus the occurrence of a parrot or of Siliceous Sponges and Crinoids in any geological stratum in high latitudes is not a convincing proof that a tropical climate prevailed during the deposition of that formation.

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Eurythermal animals are of even less value in forming an opinion on the subject, since it is well known that they are especially characterised by the extraordinary adaptability that they sometimes display to very different and remote extremes of temperature. If we are bent on reconstructing the mode of life of fossil forms, and their climatic conditions of existence, by comparison with allied living forms, land-animals must be decidedly preferred to water-animals; but even these, as it seems to me, offer absolutely no certain evidence. At most this mode of comparison can only apply when the fossil and living animals are so closely similar that we are forced to regard them as identical. This is known to be the case with the animals of what is known as the Glacial Period; but, as soon as we reach the deeper strata, and the identity of the species with those now living ceases, our right to construct a theory of the climate of past epochs by a comparison of fossil and living species entirely disappears. The very generally received opinion that such a reconstruction is possible rests in part on the old, but absolutely false, idea that certain absolute degrees of warmth, and particularly the mean annual temperature, have a definite effect on the life of animals; and, secondly, on the indisputable fact that the climatic difference of two countries always goes hand in hand with a dissimilarity in their fauna. But it ought not to have been forgotten that the daily and annual variations of temperature are not the only means which Nature has had at her disposal for the selection of species and the geographical limitation or distribution of particular forms in successive geological periods; it ought to have been duly considered that, when a change of temperature is introduced in any locality, the influence, whether favourable or unfavourable, that it may have on the mode of life or even on the existence of the animals may often be completely neutralised by the effects[55] of other conditions of existence in no way depending on the temperature and its variations.

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CHAPTER V.

THE INFLUENCE OF STAGNANT WATER.

THE media surrounding the animal, and in which it lives, are sometimes gaseous, as the atmosphere, sometimes fluid, as the water of the sea or of rivers, sometimes even solid; these last, as earth, wood, stone, &c., may be considered as absolutely motionless with regard to the animal, since they can only influence the creatures that live in them by their varying hardness or their chemical changes. Gaseous or fluid media cannot be regarded as perfectly inactive; they are capable of certain swift modes of motion, known as currents or as winds. Hence we are compelled to investigate the influences of water and air on the animals that live in them under two separate heads, according to whether the air or water is stagnant or in motion, since they influence animals quite differently in these two different states. Moreover, we must separate our enquiries as to the effects of air from those as to the effects of water, for they affect the animal world very differently. I shall begin the discussion of the whole subject with such facts and experiments as illustrate the selective or transforming influence of stagnant water.

I. General preliminary remarks.—Water is an indispensable condition of animal life. A frozen-up frog, fish, or egg of an insect is leading only a latent, not an active life. In protoplasm, the essential living constituent of every animal cell, there is a great quantity of water; if it is all extracted by drying, the cell ceases to live. The old statement is well known, 'Corpora non agunt nisi fluida.' But the universal effects of a condition of life which is equally indispensable to a single cell

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and to a whole organism are of no particularly prominent interest to the question we are discussing; on the other hand, it will be necessary to investigate a number of special instances of the effects of water more closely, in order to be able to contrast those cases in which it gives rise merely to a selection between different forms with others which prove that its influence is also capable of causing a true transformation. Few as these latter cases are, for that very reason they have special claim on our interest.

II. Effects of the chemical composition of the water.—In proceeding to investigate these, it will be well in the first place to direct our attention to two extreme cases—to the influence, that is to say, of fresh and salt water.

The salt savour of sea-water is occasioned, as is well known, by the presence of a tolerably large proportion of sodic chloride, generally known as common salt. When we speak of the effects of sea-water on animal life, they are usually ascribed to this salt. Still, as many other substances are found in the sea besides sodic chloride, such as calcium salts, magnesium salts, bromine, iodine, and other metals, carbonic acid, &c., it is to be supposed that these are not wholly without importance in the economy of animal life in the sea. But we do not know how great their effects may be; and as we are now perfectly accustomed to attribute all the differences which have been observed in the effects of sea-water, as distinguished from fresh water, simply to its saltness, and to express the difference between them in fractions per cent. of the amount of sodic chloride held in solution, we will follow the usual custom in our enquiry, without forgetting that at the same time numerous other matters add their effects, though these are unknown, to those of the pure sodic chloride.

At the first glance we might feel inclined to explain the fact, that a much greater multiplicity of forms prevails in the sea than in fresh water, by the supposition that the salt in the ocean favours the production of variety in animals. It is known that in recent times whole groups of animals are wholly excluded from fresh waters, as the Echinodermata, Sipunculidæ, polychætous Annelida, Tunicata, Brachiopoda, and Cephalopoda,

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while other groups include very few fresh-water species; to these last belong the Sponges, of which only one genus, and the Polyps (Cœlenterata), of which only two genera, inhabit fresh water; besides these, two families of Bryozoa and two of Annelida are fresh-water forms. Other groups, again, have as many representatives in salt as in fresh water. On the other hand, only one single class inhabits fresh water exclusively, the Amphibia. If we consider the smaller groups, families, or genera, we certainly meet with several typical fresh-water forms; to these belong *Melania*, *Neritina*, the *Planorbidæ*, *Limnæidæ*, *Unionidæ*, and *Anodontidæ*, among the Mollusca; the *Astacidæ* and *Asellidæ* among the Crustaceans; *Phylactolæmata* among the Bryozoa; the true leeches, *Naididæ*, *Tubifex*, and *Chætogaster*, among the Annelida; the *Cyprinoidæ* among the fishes, &c. But their number is insignificant compared with the enormous number of families typical of the sea and living in it exclusively.

Thus the fact that a much greater abundance of different forms is to be found in the sea than in fresh water is absolutely beyond dispute. But it is doubtful whether this wealth of forms does actually result, as has been supposed, from the great quantity of salt contained in sea-water. The possibility that it is so must of course be conceded, and I shall even adduce certain facts which tend to prove the justness or the probability of this view; but it must not be forgotten, in the first place, that the sea covers three-fourths of the surface of the globe, and so offers an infinitely wider surface for the development of animal forms than is offered by fresh-water lakes and streams. This circumstance alone would account for the greater multiplicity of the marine forms. In the second place it must not be forgotten that the animal life on our globe apparently originated in the sea, and that therefore the oceanic world of animal life has had a history of development of much longer (geological) duration than the fresh-water fauna; thirdly, that the influence of natural selection in fresh water is much stronger than in the sea, if only by reason of the abrupt variations of temperature; and finally—if we assume that animal life originally took its rise in the sea—that only such sea-creatures could accustom themselves to living in fresh water as were

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good swimmers, and as were eurythermal, and that they must not have been subjected to the injurious influence of a sudden change of food and sudden transfer to the salt elements of sea-water. It is commonly said—to give one special instance—that the rich variety of forms in the fauna of the Red Sea and the Mediterranean is caused by their high degree of saltness. The former is 4·31 per cent., and the second 3·79 per cent., at the surface; but this leaves out of account the fact that a merely superficial current pours in incessantly through the narrow straits which, in each case, divide the sea from the adjoining ocean, while a contrary current at the bottom of the sea carries the waters of the inland sea back to the ocean. Since, therefore, most swimming creatures, and particularly the larvæ of non-migratory animals, swim close to the surface, many more creatures in both seas must be brought in than are carried out, and thus the rich variety of forms in them may certainly quite as likely be caused by the direction of these currents as by their greater saltness.

In the total absence of all experiments directed to these points, we may set aside such vague speculations and pass on to the discussion of those facts which seem to prove that no perfectly hard and fast line of demarcation exists between fresh-water and marine animals, and that it is not absolutely impossible to accustom them to live in the element to which respectively they are strangers. The general importance of this question requires that we should enter into particulars.

A. Fresh-water animals that live in the sea.—We are accustomed to give the name simply of fresh-water animals to such groups, species, genera, families, or orders, as live exclusively or almost exclusively in fresh water. It is evident that if they were to migrate into the sea they would be exposed to a certain effect from the salt, and it may even be supposed that this effect might be injurious and strong enough to make it quite impossible for a fresh-water animal that had migrated into the sea to continue to live. However, there are a great number of so-called fresh-water forms which do actually live in the sea, some as visitors and some as constant inhabitants. It can hardly be necessary here to remind the reader of the well-known

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migratory fish—the salmon, the eels, many herrings, p'aice, and others. More interesting, because less generally known, are the cases of marine Insects or insect larvæ. Slabber has described the larva of a fly which lives in the sea, and I myself frequently met with a similar one in the Philippine and China seas; Audouin studied the habits of a beetle (*Blemus flavescens*) which lives in the sea like the fresh-water spider, *Argyroneta aquatica*; Packard has given a list of the insects which occur in the salt waters of North America, and he enumerates as belonging to them not less than ten different species of beetles, flies, and bugs. In the Pacific Ocean and Philippine Sea, I have myself often found various Insects and even Spiders in the sea,

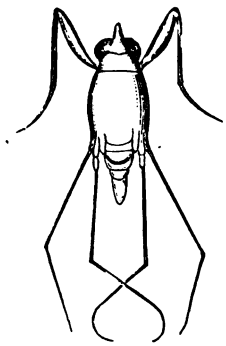

FIG. 35.—*Halobates* sp., caught by me far from land in the China Sea.

sometimes swimming in great numbers on the surface, sometimes creeping between rocks under water by the shore. A bug of the genus *Halobates* (fig. 35) is particularly common in these seas, besides the above-mentioned larvæ of flies. This genus was discovered by Eschscholtz, and now includes fourteen species living in seas the most remote from each other. The species in question runs about like our Water-Bug, *Hydrometra*, in great numbers and in every stage of development, on the high seas hundreds of miles from land. Among Mollusca a species of *Unio* lives in the Brisbane River within reach of the flood-tide. Dr. Carpenter found *Planorbis glaber* (Jeffreys) at a depth of 1,415 fathoms at Cape Teneriffe. *Neritina viridis*, in the West

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Indies, has long been known, which, like *Neritina Matonia* (Risso) at Nice, lives in the sea. I brought a great number of marine Neritinæ from the Philippines, the Pelew Islands and China, which from their variations are of the highest interest. I have also found a few species of *Melania* in brackish water; several species of *Limnæa* and a *Neritina* live at Bornholm in the Baltic, in spots where the water contains from 1 to 1·5 per cent. of salt. The Oligochætous Annelida, to which the earth-worm belongs, are typical fresh-water or land forms; nevertheless, at least nine or ten species are known which live on the sea-shore in salt water; they belong to the genera *Sœnuris*,

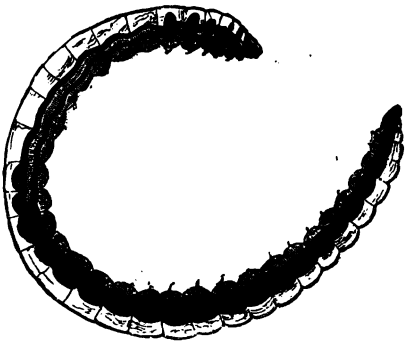

FIG. 36.—*Pachydrilus* sp., living in the Salines of Kissingen. It belongs to a group of worms, *Oligochæta*, which is principally confined to fresh water.

Enchytræus, *Tubifex*, and others. Marion, at Marseilles, has discovered a new genus nearly allied to the common earth-worm, which he has called *Pontodrilus*; this worm lives there under stones and decaying tangle, far from all fresh water, and below high-water mark, so that it is apparently alternately moistened by salt water and fresh (rain) water. In the very strong brine springs of Kissingen, I myself have found a new species of the genus *Pachydrilus* (fig. 36), of which Claparède found another species—on which he founded the genus—in the brine of Kreuznach; they are remarkably near to the fresh-water form, *Tubifex*. Finally, I will mention that the common stickleback, *Gasterosteus aculeatus*, which usually lives in

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fresh water, lives and thrives perfectly in the Bay of Kiel as well as in the North Sea, and specimens of this fish, caught at Würzburg in the month of May, were even placed at once in sea-water without sustaining any injury.[56]

B. Marine animals in fresh water.—Cases of this sort are just as frequent as those we have just been discussing, and occur among both the Vertebrata and Invertebrata. Among the Vertebrata we must first mention the American Manatus, which lives in the great rivers of South America, hundreds of miles from the sea; then a true dolphin of the genus *Globiocephalus*, which is found far inland in the Irawady river, 600 miles from the sea, and which is quite different from *Globioce-*

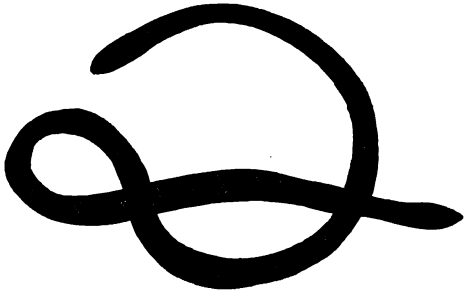

FIG. 37.—*Platurus vulcanicus*, a water-snake living in the fresh-water lake of Taal (Luzon), and having a paddle-like tail.

phalus indicus, which lives in the Indian Ocean. Among the reptiles the family of *Hydrophidæ* contains only sea-snakes, which are very common in the seas of the eastern hemisphere, and are often found there swimming in the high seas; it is only at breeding-time that they go to land.[57] The only exception to this rule is found in a new species—here represented for the first time—of the genus *Platurus* (fig. 37), which I myself discovered in the fresh-water lake of Taal in Luzon, which is famous for its still active volcano; it is true that this lake is connected with the sea by a not very long river. Together with this snake and associated with typical fresh-water forms—as *Neritina*, *Melania*, *Palæmon*, &c.—other marine animals are found, such as *Pristis Perrotteti* (the saw-fish), which is very

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common also in the magnificent Laguna de Bay near Manila. Sea-fishes, which normally live also in fresh water, or which thrive well when introduced into it, are by no means rare; thus Peters found Rays deep in the heart of East Africa; the Lake of Acqua, near Padua, which is of pure fresh water, has become famous by the success of an attempt made there to breed sea-fish—*Mugil* (the grey mullet) and *Labrax* (the basse)—in great numbers for the market. Among the Invertebrata such cases are yet more common. *Palæmon*, a genus of Crustaceans which inhabit fresh water almost exclusively, belongs to a family which generally includes none but marine animals; various species of this genus live in rushing mountain streams in the Philippines, and are found at an elevation of 4,000 feet or more above the sea. In the branchial cavity of this Crustacean

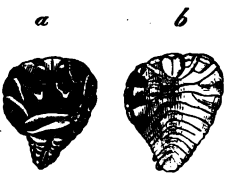

FIG. 38.—*Bopyrus ascendens*. *a*, the lower; *b*, the upper side. It lives in the gill-cavity of *Palæmon ornatus* (Oliv.), and is found with it ascending fresh-water streams at a height of 4,000 feet above the sea. All the other known species are marine.

lives a species, as yet undescribed, of the genus *Bopyrus* (fig. 38), which I have named *Bopyrus ascendens*. It is the only fresh-water form hitherto known, while the other very numerous species live exclusively in the branchial cavities of sea crabs. Aucapitaine states that a true *Cyprœa*—the species known as the money-cowry—is caught in the interior of Africa, near Timbuctoo, in quantities by the natives; various molluscs of the family of ship-borers—*Nausitara Dunlopi* (Wright) and *Teredo senegalensis* (Blain.)—and of the Pholadidæ—*Martesia rivicola*—live in the rivers of India and Java, while all the other species of these families are true marine creatures. I ate oysters (fig. 39) at Basilan in the south of Mindanao, which, although they had a salt flavour and were indeed bathed by brackish water at high tide, yet at ebb tide were surrounded

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by a rapid stream of pure drinkable fresh-water, and opened their shells to it. Many marine Bryozoa occur also in fresh water. Among the Annelida the case seems to be rarer, and I have only been able to find one instance mentioned in books by Leidy, who discovered a worm, *Manayunkia*, belonging to the Cephalobranchiata, in the Schuylkill River, near Philadelphia. The Nemertine worms, so common in the sea, have only one representative in fresh water of certainly a very divergent form; of Sponges we find only one genus, *Spongilla*; of the Hydroids only two, *Hydra* and *Cordylophora* (fig. 40), which, in the course of time, have become true fresh-water animals.[58]

FIG. 39.—Oyster from the Cumalaran River at Basilan (south of Mindanao); it lives in spots where the water is quite fresh

C. The effect of the different percentage of salt in the water.—The cases adduced above prove that it is often impossible to distinguish, by systematic characters alone, whether an animal is fresh-water or marine, since there are many species in fresh water whose nearest allies live in the sea, and *vice versa*. Theoretically, then, we must admit that there is no general and insuperable impossibility that they should exchange their life in one medium for that in the other. But this theoretical possibility is not, so far as we know, universally practical; for whole groups—as the Brachiopoda, Sipunculidæ, and Echinodermata—have hitherto been found only in the sea. The question now is: What causes have prevented or still prevent a transfer of marine animals from sea-water to fresh

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water, or *vice versa*, from actually taking place much more frequently?

I have already indicated that very often the strength of the current in a river, or the surf at its mouth, its temperature or the kind of food it affords, must cause quite as great hindrances to the passage of a marine animal into the fresh water as the necessity for subsequently living in water devoid of salt. Thus, for instance, the remarkably tender bodies of the larvæ of the Echinodermata, Ascidiæ, sea-anemones, Hydroid polyps, and others, are scarcely fitted to overcome such impediments; so that, even under the assumption that they might be capable of living in water without salt, their transfer into fresh water seems to be almost impossible; and this is still more probably the case when the fully grown creatures—such as Ascidians, Corals, Polyps, and others—do not move freely on the sea-bottom, but are permanently attached to it. But if we now leave out of the question the other influences which are often combined with the variable amount of salt in the water, and which shall be discussed in another place, we have in the first place to determine the optimum as well as the extreme proportion of salt in the water which may be advantageous to different animals, so as to be able to estimate how far variations in its saltness may have a selective influence on those living in it or migrating into it. Secondly, we must deal with the question whether and how far an alteration in the salt contents of the water is capable of directly modifying the morphological characters of a species. But first of all we must ascertain the mode by which the salt held in solution in the water penetrates to the interior of the body, where alone it can produce any effect.

Claude Bernard has proved that salt, when in solution in water, can penetrate the body of an animal without the creature's agency, merely by the endosmotic action of the skin. If a frog is placed in a vessel in salt water, in such a position that it cannot swallow any salt, it will nevertheless be found that its body soon contains salt. If it absorbs more than it can bear, it will die, and its death will ensue all the sooner, the stronger the solution is in the first instance. In order to determine what is the minimum percentage of salt

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that is, on the whole, injurious to the frog, I made a variety of experiments in the following manner. To prevent the creature from swallowing, and so dying of suffocation, I tied it to weighted sticks in such a way that it was unable to dip its nose and mouth into the water, even when its head began to sink from weakness of the muscles. A great number of frogs were placed in different vessels, each containing the same quantity of water with various, but known, amounts of salt in solution; death was assumed to have taken place when the eyelids of the frogs no longer reacted under irritation, and did not recover their sensibility after the creature was taken out of the salt water and washed in fresh water. By this I found that a frog commonly died, on an average, in about two hours and a half in a solution of five per cent. of salt, in three hours in three and a half per cent., in almost seven hours in two per cent., and not before more than twenty-four hours had elapsed in one and a half per cent. They all, without exception, endured a solution of one per cent. without sustaining any injury; that is to say, they lived as long in their very uncomfortable position as other frogs which were fastened up in the same way in pure fresh water—namely, from three to four days. It remains still doubtful, therefore, whether a frog cannot really live just as well in water with one per cent. of salt in it as in fresh water. I have not made any experiments on this point. But near Greifswald, on the Baltic, frogs live and spawn, as I have learned from my assistant, Dr. Braun; so it is highly probable that a solution of one per cent. of salt in the water is about the limit of where it begins to be injurious to frogs. Similar experiments have been made by Plateau on aquatic Articulata, and he seems not to entertain the slightest doubt that in this case also the salt penetrates through the skin; although, when the animals are completely immersed in the water, imbibition through the mouth does not seem to be excluded. But as aquatic Articulata cannot die of suffocation so long as the water contains a sufficient quantity of air, or as the animal is allowed to rise to the surface to breathe, this question is of no practical importance to us. The most important result established by the above-mentioned experiments, and by Plateau's, is this: that the behaviour

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of different animals under the effects of the same degree of concentration in the salt solution is by no means identical; the maximum of strength which is perfectly innocuous to the frog is about one per cent., while the stickleback can bear from two to two and a half per cent.; migratory fish, as the shad, salmon, eel, &c., have still greater powers of resistance, as they can bear as much as from three and a half to four per cent. of salt in the water.[59]

It results from this, that the difference in the osmotic action of the skin in different animals, and the various degrees of resistance to the amount of salt absorbed into their tissues, connected with such a difference, do, in a certain sense, cause and maintain the distinction which prevails between the fauna of the ocean on the one hand, and that of rivers and fresh-water lakes on the other. We may assume that the absorption of salt is most rapid in animals with a soft skin; we are not surprised when we find that the soft gelatinous Medusa is almost instantaneously killed on coming into contact with fresh water, while crocodiles with their strong and horny scaly covering, through which salt, as it would seem, cannot penetrate, can live equally well in the sea and in fresh water. Between these two extremes the gradations are infinite. Every variation in the amount of salt in fresh or salt water must therefore influence the animals living in it in a different manner; some will be killed, others checked in depositing their eggs or hindered in their growth, while others will bear the change without any injury. It would be a very interesting problem to determine by exact experiments a curve showing the resistance of different species to the absorption of salt by the osmotic action of the skin.

Unfortunately hardly any such experiments are on record; but the few that are before us offer so much that is of interest, even under the scarcely exhaustive treatment they have met with, that we must here go into them somewhat more closely.

In the first place an experiment must be mentioned which Nature herself has made on a certain Polyp. It is, so far as I know, the only example of an animal that can be proved to have originally lived in the sea, or in brackish water, and which, within our own time, has gradually accustomed itself to

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live in pure fresh water. When I was still a student, *Cordylophora lacustris* (fig. 40) was found only in estuaries and at the mouths of rivers where the water was at any rate occasionally salt or brackish; it was discovered almost simultaneously in England and Belgium, and somewhat later I found it in the Schlei, near Schleswig. Since that time, 1854, the animal has in many places migrated into rivers; it has already reached the Seine at Paris, and has got into the fresh-

FIG. 40.—*Cordylophora lacustris* (from F. E. Schultze), a brackish-water polyp which within the last ten years has gradually migrated into pure fresh water.

water aquarium of the Jardin des Plantes there, where it is said to be very common. Its migrations in the Elbe were still more remarkable. After reaching Hamburg, and even, if I am not mistaken, finding its way into the Alster, it took possession at the same time of the great water-pipes of the city, in which it lived, associated with the well-known bivalve, *Dreissena polymorpha*, in such enormous quantities as to impede the flow of water through the pipes. This case is the more interesting

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because the Cordylophora is a quite soft animal of the Polyp group, and yet it could quickly become accustomed to a diminution of salt in the water which would, beyond a doubt, entirely destroy many apparently stronger animals. It would probably be of much assistance and interest to compare examples of Cordylophora from different localities, to see whether, perhaps, the variations in the mode of life have not given rise to some variation in the structure of the animals living under different conditions. This point has not, so far as I know, hitherto been closely investigated.

Only three series of experiments are known to me, which were made under artificial conditions, with the express purpose of determining what animals could bear a transfer from salt to fresh water and *vice versa*. The experiments made long ago by Beudant have never hitherto been repeated. He found that various fresh-water molluscs were quickly killed if they were suddenly transferred from fresh water to the concentrated salt water of the Mediterranean; but when he increased the amount of salt very gradually he obtained very different results. He began in April by putting animals into water which contained only one per cent. of salt, and by September, by gradual additions of salt, he had brought it to a solution of about four per cent. Species of the genera *Limnæa*, *Physa*, *Planorbis*, and *Ancylus*, lived in this salt water as well as in pure fresh water, while of *Paludina vivipara*, *Bythinia tentaculata*, and *Neritina fluviatilis*, a much greater number of individuals had died in the salt water than in the fresh water. Of bivalves—*Unio*, *Anodonta*, *Cyclas*—every specimen had perished before the water had reached its highest strength of four per cent. He subsequently conducted the experiments in the inverse order at Marseilles, placing true marine animals in fresh water. He then found that a sudden transfer killed almost every species, while gradual additions of fresh water to the salt were borne by many species, till in the course of a few months it had become perfectly fresh, so that finally true marine animals were living with *Limnæa* and *Planorbis*. The edible mussel seemed particularly resistent, for not one single specimen perished throughout the whole duration of the experiments. Of 610 indivi-

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duals of various species which were gradually accustomed to fresh water, only 37 per cent. died, while of a corresponding number which were kept at the same time constantly in sea-water 34 per cent. died. Thus the percentage of mortality in the group of animals that were gradually accustomed to a foreign element was only three per cent. higher than in those which remained in their natural element. Certainly it must be considered that this result was due to the circumstance that certain species—as *Mytilus*—remained altogether unaffected, while others died out entirely. For further details I refer the reader to the note.[60]

We perceive from these experiments of Beudant's that some species of Molluscs can live equally well in fresh and salt water, although they may be exclusively fresh-water or marine forms. Unfortunately the experiments have not been carried out far enough for us to be able to draw any far-reaching conclusions from them. Beudant, it is true, proved that a fully grown *Mytilus* could be accustomed to fresh water, but not that it could multiply in it. Granting that a gradual transformation of the salt water in the Baltic into fresh water could take place, according to Beudant's experiments a number of full-grown or half-grown animals might become accustomed to the fresh water; but the species might nevertheless very possibly die out, particularly if their eggs and larvæ were not equally capable of surviving in fresh water. In the quaternary period numerous oyster-beds existed in the Baltic which have since then entirely disappeared;[61] and yet the oyster belongs, according to Beudant's tables, to those forms which are able to live almost as well in pure fresh water as in salt water. The extinction of the oyster in the Baltic may have resulted, as must certainly be admitted, from a variety of causes; but in view of the total absence of all means of proof we must not reject as unfounded the assumption that it was caused by the incapacity of the young oyster-larvæ to withstand the injurious effects of the diminution of salt in the Baltic.

Plateau went somewhat further than Beudant in his researches on the aquatic Articulata. His experiments on the common Water-Louse (*Asellus aquaticus*) are particularly interest-

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ing. By accustoming fully grown specimens of this species to water to which he constantly added salt, he brought them to live and lay eggs in pure sea-water. The young sea-lice born in fresh water died much sooner, according to him, than the old ones, when both together were suddenly transferred to sea-water. While the young fresh-water lice lived only five hours when put into sea-water, the young ones which had been born in water already salt lived about 108 hours. Whether they died for lack of food or from the effects of the salt is not determined. But even if we arbitrarily assume that the salt was in this case really the cause of death, it nevertheless results from the data above given that at any rate the injurious effects of the salt are different at the two different ages of the same animal; and, secondly, that the injurious effect on young individuals can be materially diminished when the older and sexually mature individuals are accustomed to the strange element and breed in it. These experiments, as well as those of Beudant, ought to be repeated in a methodical manner; but, imperfect as they are, they teach us that many aquatic animals can be accustomed to a foreign medium, and can even propagate in it. Now, although, in consequence of the imperfection of these experiments, no extensive application of this conclusion is possible, they still allow of our propounding the view that it can no longer be said to be impossible to accustom certain fresh-water species perfectly to live in the sea, or, on the other hand, marine species to live in rivers or lakes.

A still higher interest attaches to the recent experiments of Schmankewitsch. The fresh-water Crustacean, *Branchipus stagnalis* (fig. 41, *a*) is remarkably like the *Artemia salina* (fig. 41, *b*), one of a genus otherwise found exclusively in the salt lakes of America, Europe, and Africa. Nevertheless the differences between them have always seemed sufficiently conspicuous to justify their separation into two different genera; these are certain dissimilarities in the shape of the antennæ of the male, and the number and form of the posterior segments of the body, of which *Artemia* has but eight while *Branchipus* has nine.[62] There are numerous species of *Artemia* in Europe. The most unlike are *Artemia salina* and *A. Milhausenii*; the latter is distinguished

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by the absence of spines on the lobes of the tail, the small size of these lobes, and the relatively large size of the branchial appendages of the legs. Schmankewitsch showed that it was possible to raise a brood of *Artemia Milhausenii* from *Artemia salina*, which lived in salt water of 4° Beaumé, by gradually raising the percentage of salt to 25° B. This transformation occurs very gradually, and only in the course of several generations. He observed the same process also in a free state of nature. A dam which divided a lake containing salt water of 4° B. from another where the water marked 25° B. gave way in the year 1871, so that the density of the water in the lower lake fell to 8° B. At the same time numberless individuals of

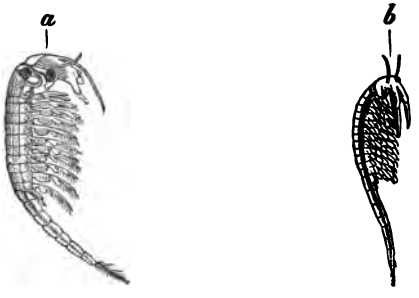

FIG. 41.—*a*, *Branchipus stagnalis*; *b*, *Artemia salina*.

Artemia salina were carried through to the lower lake by the flood, and there they soon settled and propagated. After the dam was repaired the saltness of the water in the lower lake naturally increased again; in 1872 it had risen to 14° B., in 1873 to 18° B., and by the end of September 1874 it had reached its old mark of 25° B. During this period the *Artemia salina* that had migrated had gradually become transformed into *Artemia Milhausenii*. The stages of transformation, as they were actually successively observed one after another by Schmankewitsch, are here given in a woodcut (fig. 42) copied from Schmankewitsch's drawing.

He also conducted the converse experiment with perfect

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success, for he brought *Artemia Milhausenii* back to *Artemia salina* by breeding successive generations in salt water which he made weaker and weaker. Now the differences between the two species are so great that no zoologist had previously cast any doubt on the accuracy of classing them as two species,

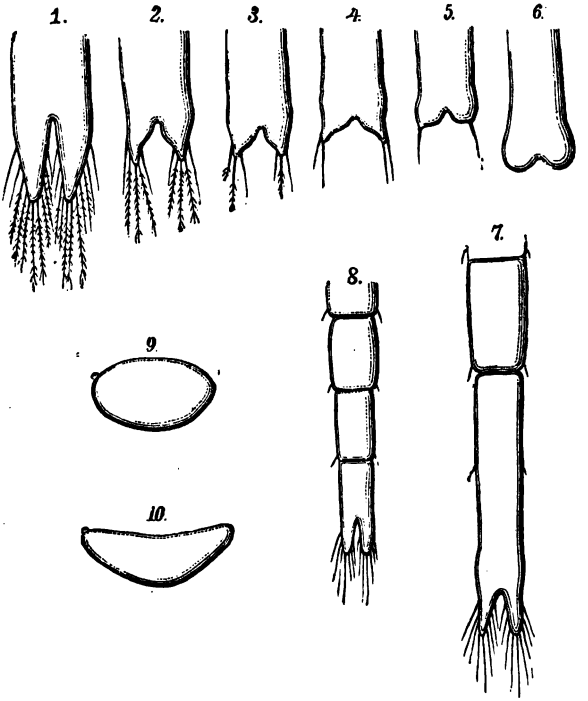

FIG. 42.—Transformation of *Artemia salina* to *A. Milhausenii*. 1, tail-lobe of *A. salina* and its transition through 2, 3, 4, 5, to 6, into that of *A. Milhausenii*. 7, postabdomen of *A. salina*; 8, postabdomen of a form bred in slightly salt water; 9, gill of *A. Milhausenii*; 10, gill of *A. salina*. From Schmankewitsch.

and with all the more reason because each seemed to exclude the other; Schmankewitsch's experiment has nevertheless proved their relationship, and also explains very simply the fact that they never occur together. It is merely the constancy of the external conditions of life—the greater or less saltness of the

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water—which in one case determines the character of *Artemia Milhausenii* and in another that of *Artemia salina*. But Schmankewitsch was so fortunate as to be able to carry the experiment still further. He kept *Artemia salina* in salt water, which he constantly diluted by adding fresh water, till at last it was perfectly fresh; the Crustaceans had meanwhile gone through several generations, and had gradually so completely changed their character that finally they had acquired those of the genus *Branchipus*.

These discoveries are certainly of the greatest interest; for they afford a proof we can scarcely doubt, that a change in the amount of salt contained in the water can produce a regularly recurring and very conspicuous modification of the specific and even of the generic characters of certain animals. Darwin's opponents will probably say that in this case those zoologists were in error who attributed to the differences between *Artemia Milhausenii*, *A. salina*, and *Branchipus stagnalis*, a specific and even a generic value, and that all these forms must now be regarded merely as varieties of one single species, since proof has been given that they pass into each other. It is no part of my purpose here to oppose such a view of the case; it will suffice to observe, on the other hand, that, logically speaking, writers on Crustaceans must then cease to have any justification for separating or describing species at all, since those differences between *Branchipus* and *Artemia* which, according to this view, have neither specific nor generic value are precisely those of which they constantly avail themselves for distinguishing the species and genera when describing other Crustaceans.

Thus evidence has been given in this chapter that changes in the degree of saltness of the water exert not merely a selective influence on the animals exposed to them, but also sometimes effect a remarkable modification of them; and it is probable that other soluble elements in the water besides simply sodic chloride may be able to exert a similar influence. We are only at the beginning of our knowledge on this point. A careful repetition of the experiments here briefly described, with as great a variety as possible of animals and with as much thoroughness as Schmankewitsch exercised, would, beyond

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doubt, contribute many important facts. But they would certainly confirm the result obtained already: That there can be no idea that a uniform change in one definite condition of existence will produce a uniform effect on different animals.[63] This conclusion is self-evident when we reflect that the result of any influence must be the resultant of a reciprocal action of the external efficient force and of the inherent plasticity of the organism which is influenced.

III. Influence of the volume of water.—It is well known that the volume of water has a marked influence on the growth of an animal, and on the size it finally attains. Every lover of the 'gentle craft' of fishing—for salmon, trout, or other fresh-water fish—knows that these fish are usually small in small streams and lakes, and attain their full size only in large ones. This fact has often been proved in America as well as Europe. All experimental zoologists know moreover that it is often difficult, or even impossible, to rear fresh-water animals in a small aquarium to the size which they grow to under the normal conditions of a free life in rivers, ponds, or even small pools.[64] This is attributed, if not without exception, at least very generally, to a deficient food-supply. Without any experimental enquiry, and under the tacit assumption that all the other conditions—such as the temperature, the composition of the water, the amount of the oxygen it contained, and the number of individuals—were the same in the aquarium as in small ponds or large lakes, it was asserted that the smaller size of creatures in a small body of water was due solely to the circumstance that the absolute quantity of food at the disposal of each individual must necessarily be smaller in a small volume of water than in a great one, and hence be insufficient for the development of the animal's full size. Of course it cannot be disputed that a fish must remain small if the food within its reach does not attain the daily optimum. But it has never been investigated whether the small size of the creatures in a small body of water is due, without exception, to the small amount of food within reach, either by proving that this actually was less than was indispensable for the full growth of the animal, or by attempting to

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show that any other influence was impossible. Observations do exist, on the contrary, which are calculated to warn us to be cautious in this matter. I will here only refer to the fact I myself observed that some Water-Lice (*Asellus*) which were kept in an air-tight closed glass vessel for nearly two years, and produced three or four generations, were, in the last generation, abnormally small, though food, in the form of algæ and other plants, was constantly abundant, and the air above the water, on opening the vessel, was found to be perfectly pure. In this case lack of food was assuredly not the cause of the small size of the Aselli; perhaps it was a result of constant inbreeding, although in so small a number of generations—only four—this is hardly probable. Hence it is a quite unfounded assertion to say that the small size of animals in a small body of water is always the result of a consequent deficiency of food, since if this were so, whenever a more than sufficient supply of food is at hand in the small body of water, the full growth ought to be attained. But this is not always the case, which proves that the often-observed effect of the volume of water on the size of the creatures living in it is not, up to the present date, understood, and still awaits an explanation.

In order to solve this problem if possible, I carried out an extensive series of experiments on the common pond-snail, *Limnæa stagnalis*. I selected this creature because its growth is tolerably rapid in comparison with others, and because its long spiral shell offers an excellent test, of which it is easy to avail oneself in estimating its rate of growth. Moreover, this animal, as I had learned from an accidental observation, is so remarkably sensitive to the effects of the volume of the water, that, in the space of six days, the difference in the length of those living in different volumes of water could be easily and accurately determined.

It will be understood that I can in this place give only the general results of experiments carried on for more than two years.

I instituted two series of experiments—one by separating the animals from the same mass of eggs immediately they were hatched, and placing them simultaneously in unequal bodies

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of water; the other by placing two different quantities of animals, from the same mass of eggs, in two aquaria of equal size. All the conditions of existence, and above all the supply of food, were kept at the optimum. Consequently all the animals were under equally favourable conditions, irrespective only of the volume of water which fell to each animal's share; this varied at most between 100 and 2,000 cubic centimètres. In both experiments the results were similar (fig. 43): the smaller the volume of water which fell to the share of each animal, the shorter its shell remained; and, moreover, it made no difference, with regard to the length the shell attained in the different groups of animals, whether each isolated individual had from the first a definite quantity of water allowed to it, as in the first series of experiments, or whether several indi-

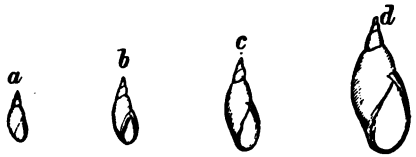

FIG. 43.—Four equally old shells of *Limnæa stagnalis*, hatched from the same mass of ova but reared in different volumes of water; *a*, in 100 cubic centimètres; *b*, in 250 cubic centimètres; *c*, in 600 cubic centimètres; and *d*, in 2,000 cubic centimètres.

viduals living together had a larger volume of water to share among them in the same proportion. Thus I succeeded, under conditions of existence otherwise identical, in establishing a curve of growth for the Limnæa corresponding to the volume of water. This curve (fig. 44) shows that the favourable effect of an increase of volume of water is highest between 100 and 500 cubic centimètres for each individual, and that it then gradually decreases, till, at 5,000 cubic centimètres, it would seem to cease entirely; *i.e.* an increase of volume above this maximum has, as it appears, no further effect whatever upon the rapidity of growth. Thus the optimum of the volume of water which allows the greatest possible length of shell to be attained by a Limnæa within a given time lies approximately between 4,000 and 5,000 cubic centimètres; to determine the point exactly was impossible for various reasons. The woodcut (fig. 43) exhibits the

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shells corresponding to this curve. The first of the shells, formed in 100 cubic centimètres of water, attained a length of only 6 millimètres; the second, in 250 cubic centimètres, was 9 millimètres long; the third, in 600 cubic centimètres, was 12 millimètres; finally the fourth grew to 18 millimètres in 2,000 cubic centimètres of water. It scarcely need be repeated that these animals, with such immense differences in length, were all the offspring of one mass of eggs simultaneously transferred, and had all reached the same age of sixty-five days.

My experiments also allowed of my constructing a curve of time for the rate of growth of the Limnæa. The reader may have observed, with reference to the foregoing statements, that according to this volume-curve it ought to be possible to

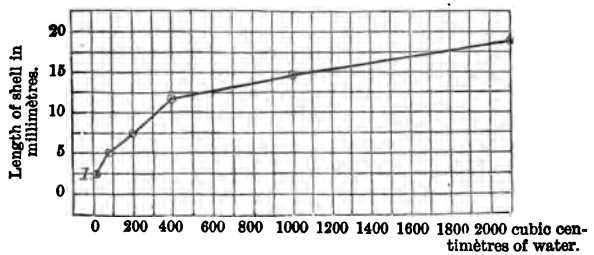

FIG. 44.—Volume-curve for *Limnæa stagnalis*.

enable a Limnæa to attain its full length of about 24 millimètres (for the first year's growth) even in a volume of 100 cubic centimètres, if only it were left there for a longer time than was requisite for acquiring that length in 2,000 cubic centimètres. Still, this would only be possible if the rate of growth, as determined by the volume of water, were at all times equal This, however, is not the case. At first the growth is very slow; then succeeds a period of quickest growth, until the older the animal is, the more slowly it grows. The curve exhibited in the subjoined woodcut (fig. 45) was constructed from experiments in a volume of water of from 1,000 to 2,000 cubic centimètres per individual, and it shows that, during the first three weeks after escaping from the egg, the growth of the young animal was, on an average, only 5 millimètres; then followed

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a period, lasting about three weeks, of very rapid growth, during which it attained a length of shell of about 10·2 millimètres; in the third period—40th to the 60th day—it grew only 6 millimètres more; and then ensued a period of very slow growth, only about 1·6 millimètre in nearly four weeks. It is thus proved that the same law obtains for Limnæa as for all other animals, namely, that the maximum of growth can only be attained, when all the other conditions are equally favourable, exactly within the period of quickest growth; the opportunity once missed never recurs. A Limnæa which in the course of the first year has not attained a length of shell

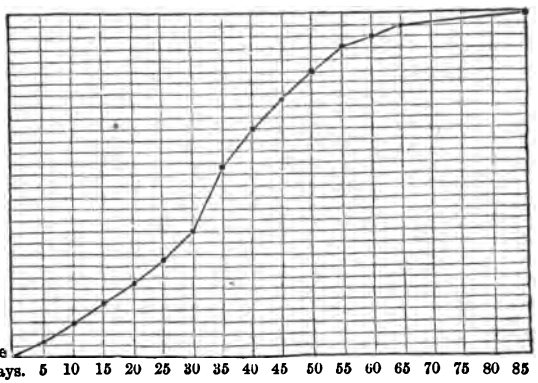

FIG. 45.—Curve of time for the growth of *Limnæa stagnalis*. The growth is most rapid from the fourth to the fifth week.

of at least 20 millimètres must become the parent of a race of dwarfs, if the causes which have checked its growth are regularly repeated in the succeeding years.

A direct influence is hereby proved to be exerted by the volume of the water, irrespective of the supply of food and other influences.[65] A short discussion of the details will show whether we are as yet in a position to determine the special causes of this effect of volume.

It is self-evident that a great variety of influences might have produced the same result—*i.e.* the dwarfing of the animals—such as food, temperature, injurious gases, or the absence of

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those that were necessary, &c. In some of my experiments such influences showed themselves very conspicuously. In one, for instance, in order to supply the young animals with the maximum of air required for respiration, I kept up a constant current in the vessel; but the experiment failed totally, because the young animals in the current were unable to cling to the plants they fed on. On another occasion a sudden and very considerable fall of temperature set in, almost down to 13° centigrade. Now this is the degree at which the powers of assimilation of the young Limnæa cease, and consequently its growth. The effect on the curve of volume was very striking (fig. 46). The vessels, of unequal size and containing unequal bodies of water, stood side by side at the same distance

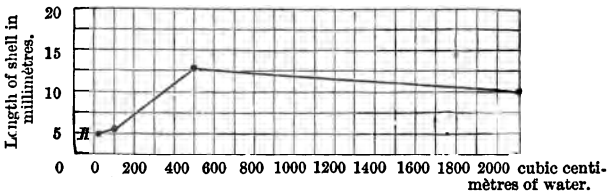

FIG. 46.—A curve of growth totally altered by a change of temperature. It continues to rise as usual up to 500 cubic centimètres of water. There it suddenly falls, because the temperature of the large body of water is insufficient to allow the Limnæidæ living in it to assimilate.

from a window, where the sun shone in the afternoon for two hours at the most; thus the temperature favourable to assimilation was attained in the smaller vessels, but not in the larger ones. Hence it followed that snails which lived in 2,000 cubic centimètres of water, and consequently ought already to have been 10 millimètres long when 25 days old, were scarcely longer—about 3 millimètres—than those which had lived in water which, though less in volume, was sufficiently warm. At the same time the nourishment provided in each vessel was so abundant and wholesome that neither bad air nor a lack of food could have occasioned the striking break in the normal volume-curve; besides, in that case the effects must have been visible in those in the small as well as those in the larger body of water.

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A superabundance of food was purposely supplied throughout all the experiments, and all the glasses in which the food-plants—*Alyæ*, *Elodea canadensis*, and *Lemna*—did not grow luxuriantly were emptied, so that from the very first, in all the experiments on which the curves were founded, the injurious effects of any kind of dearth of food were excluded.

The temperature of the water, so long as it oscillates within an insignificant range near the optimum, also has no effect on the volume-curve, or at any rate a very trifling one; if the influence of volume had been affected by variations in the temperature of the water, all the animals in the various experiments growing up in different bodies of water, so long as they were at a similar temperature, must have attained the same or nearly the same size. Temperature does not exercise a really decisive influence till it approaches one of the two utmost endurable extremes.

It might also be supposed that the different proportions of oxygenated air or carbonic acid contained in the water were the efficient cause; but this is easily disproved. In the first place, it is not very easy to see how, in that case, such regular curves of volume could arise, since the deficiency of air in each vessel must then have been always in the same proportion as the body of water; and this can scarcely be assumed as probable. On the other hand, this influence was already excluded by the fact that the superabundance of plants growing in the water disengaged so much oxygen that the water in all the glasses must have been absolutely saturated with it, and the stratum of air in contact with the surface, which, as is well known, is breathed by the Limnæa, must have been equally and perfectly pure. For the same reason the carbonic acid disengaged by the animals must always have been entirely reabsorbed by the plants.

The salts which can be proved to be present in water can just as little be regarded as the cause of the dwarfed growth of the animals. With the assistance of a chemist, my friend Professor Hilger of Erlangen, I repeated my experiments with distilled water, and with water which was saturated with the constituents proved normally to occur in water (such as magnesic sulphate, calcic carbonate, &c.), and the normal course

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which regularly ensued showed that the salts present and discoverable by chemical tests had really no influence that could be detected.

Even injurious gases which might be formed, in a certain proportion to the body of water and the number of animals, from the fæces and other decomposing organic matter, cannot be regarded as causing the effects referable to the volume of water. Suppose we take two vessels containing equal volumes of water, but place only one animal in one and twenty in the other, these last of course will disengage the larger amount of injurious gases, and consequently, in the first instance, a certain retardation in their growth might be caused. But since the one isolated individual grows immensely faster than those that live together, this one will very soon yield as much, and at last more, fæcal matter than the twenty; so that growth must cease with it at least as soon as with the others. But since this is precisely not the case—for the curve of time remains the same for each, while it is only the size attained within a determined period which varies—it is, it seems to me, thereby proved that the effects of the injurious gases produced by the animals themselves cannot be the cause of the effects of volume.

What, then, is the real cause? I regret to say that I cannot give any answer to this question. With the assistance of my friend Hilger I have long been trying, but altogether in vain, to find anything present whatever, even in the smallest quantity, to which this effect of volume could be ascribed. I think, however, that we are justified in the following hypothesis. It would seem to follow from my experiments that some substance —as yet unknown—must be present in the water, probably in a very minute quantity, which, by its relations to the water that holds it in solution and by its osmotic affinity to the skin of the animal, can be absorbed only in a determined and extremely small quantity, and also within a definite period and in a definite amount of water.[66] Now, if this substance were simply a stimulant, and thus, without actually contributing to growth, were nevertheless essential to it—like the oil to the steam-engine—it must be absorbed in the quantity which is most favourable if the normal growth is to be accomplished within a fixed time.

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And since, according to this hypothesis, the amount of the substance absorbable in a given time depends on the volume of the water, and increases or diminishes with it, growth would cease entirely if the body of water were so small that it had a stronger affinity to the unknown matter than the skin of the animal has. On the other hand, the attainment of the full size within the corresponding period would only be possible if the volume of water were so great that the Limnæa could at all times absorb this unknown stimulant from the water.[67]

IV. Influence of oxygen or air in the water.—We have seen in the foregoing sections that the effect of the substances held in solution in the water, and also apparently that of the volume of the water, depend on the osmotic action of the animal's skin. Another substance held in solution in the water must take effect in a precisely similar manner—namely, the air used up in breathing by a number of animals. It is known that every animal, even the simplest Infusorium that lives in water, requires air, or rather oxygen, for respiration; and as most aquatic animals have no special organs for breathing in the air itself—like most of the Vertebrata, as well as Insects, Arachnoidæ, Myriapoda, and many other creatures—their efficient respiration depends exclusively on the absorption of the air (oxygen) contained in solution in the water through the skin, or through the membranes of some internal organs through which water flows in and out in a constant stream.

It is self-evident that every growing or young cell must be capable of breathing, *i.e.* of taking in oxygen and disengaging carbonic acid, if this respiration is a function of protoplasm itself. All growing parts which are in contact with media rich in oxygen, such as air and water, must consequently breathe,[68] taking it for granted that their surface offers no resistance to the absorption of oxygen. But the disposition to absorb it may be very different in different parts of the body; and we are accustomed to call such parts as seem better fitted to absorb oxygen, as compared with the others, simply 'organs of respiration.'

Such specialised organs of most of the animals that live in water and breathe water [69] are, in the first place, the skin, then

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appendages of the skin, known as gills or branchiæ, and finally the interior of the intestinal canal. In very many Invertebrate animals—as in Holothuria, Annelida, Planarians, Water-Insects, and others—a constant stream of water enters by the anus, and

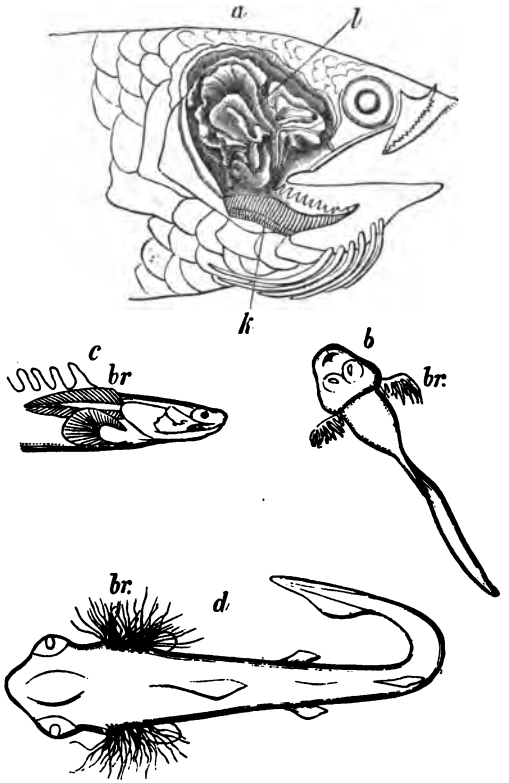

FIG. 47.—*a*, *Anabas scandens*; head, with *k* the gill-cavity laid open, and *l* the contiguous cavity containing the foliated labyrinthine structure. *b*, Tadpole; *c*, young Polypteru from the Nile; *d*, embryo of the Shark. All these have external gills, *br*.

in a few cases, as in Holothuria, a very easily demonstrable stream passes out from it also. Thus, in the simplest condition, the mucous membrane of the intestine serves for respiration, like the skin of an animal; and in this respect the well-known

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French physiologist, Paul Bert, is perfectly right when he says that any dispute as to whether this or that portion of the body of an animal is its respiratory organ is fundamentally and perfectly superfluous. But when special appendages are developed from the skin in a foliated or arborescent form—known as gills—which seem specially adapted by their structure and the delicacy of their walls to absorb more air from a given body of water than the skin can, and to transmit it directly to the blood or to the fluid of the body-cavity which circulates in those gills, we are certainly quite justified in designating these appendages as special organs of respiration.

Such gills or branchiæ occur in the intestine as well as on the skin of the most dissimilar animals living in water.

The gills of the outer skin bear so striking a relation to the animal's mode of life that they must here be briefly discussed. In Fishes (fig. 47, *a*) and in many Amphibia the gills are placed at the side of the head or partially under it, where they are concealed beneath larger or smaller folds of the skin, which, with the flat bones that support them, are known as the gill-covering. In the embryo of the Shark (fig. 47, *b*, *d*) and of Amphibia, external ramified gills appear before these internal gills; these, in the fishes, subsequently disappear, but in the Amphibia persist throughout life (*Perennibranchiata*). In Crustaceans we often find gills in places analogous to their position in fishes, that is to say, by the side of the cephalothorax, and covered by a large skin-fold attached to it; this is the case in Crabs (*Brachyura*), and in many of the Macroura, Lobsters, Prawns, &c. In other Crustaceans, on the contrary, as in our Water-lice (*Asellus*) or the Sea-louse (*Idotea*), they are situated at the end of the abdomen, and in yet other species they are appendages of the legs, whatever part of the body these may be attached to. In the class of Mollusca we find not less than five forms of gills morphologically different—first, the usual gills of bivalves (fig. 48, *b*); secondly, those borne on the back of many of the naked marine Mollusca, as the *Æolidæ*, *Doris*, and others (fig. 48, *d*); thirdly, the dorsal branchial cavities of such genera as *Neritina* and *Melania*; fourthly, lateral gills, as in *Phyllidia*; and lastly, the highly interesting mantle-gills of

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some species of *Lucina* (fig. 48, *a*), situated on the ventral margin of the mantle. In the Annelida the gills are usually an appendage of the legs, and sometimes are placed directly on the body or at the fore end, as in *Sabella*, *Serpula*, *Terebella*, &c. Finally, the number of Invertebrata is by no means small which dispense entirely with such distinct, conspicuous organs

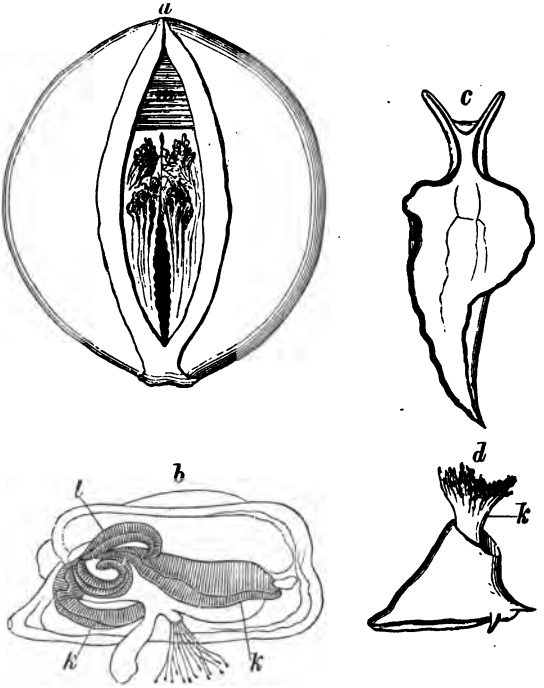

FIG. 48.—Gills of Mollusca. *a*, *Lucina philippensis*, with four mantle-gills behind the muscle *m*; *b*, Mytilus, with *k* the gills, and *l* the laminated lip; *c*, *Elysia grandis* (Bergh.), destitute of gills; *d*, *Doris* sp., with a tall tuft of dorsal branchiæ.

of respiration, and consequently breathe only through the skin; among the Mollusca there are the *Elysiadæ* (fig. 48, *c*) and their allies; among the Annelida the common leech and the Oligochætæ (the earth-worm, &c.); many of the lower Crustaceans—parasitical as well as independent—all Infusoria, the Cœlenterata, and even many Echinodermata, &c.

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Less variety is found among the internal gills, which sometimes are situated in the intestinal canal of water-animals. In the larvæ of the Libellulidæ, for instance, leaf-shaped organs are found inside the rectum, which apparently serve for respiration. I myself have described a system of foliated processes on the mucous membrane of the stomach of the Holothuridæ (fig. 49) which have all the attributes of true gills—as an extensive surface, delicate membrane, and abundant blood-vessels, with a constant renewal of the water that bathes the laminæ. In most Annelida and many other Invertebrata, no

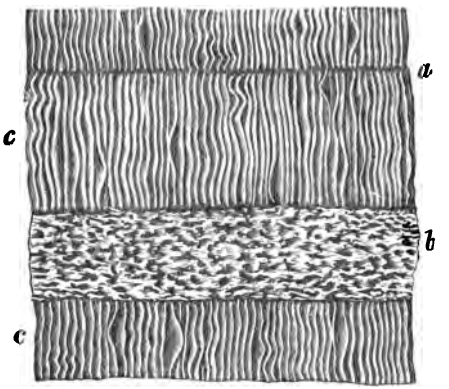

FIG. 49.—Part of the stomach of a Holothurian (*Stichopus variegatus*) split open lengthwise and laid flat. *a*, the dorsal furrow between the two series of gill-foliations; *b*, the broad tumid ventral surface which divides them; *c*, the foliaceous gills.

doubt a regular current of constantly renewed water passes through the intestine, which nevertheless bears no special gills; the more or less extensive folds of the mucous membrane here take the place of the absent organs. It may here be incidentally mentioned that even a fish (*Cobitis fossilis*, a species of Loach, fig. 50) breathes through the intestines; but in this case the conditions are slightly different, inasmuch as it takes in air-bubbles at the surface of the water through its mouth, and swallows them, so that here the air comes into direct contact with the respiratory surface of the intestine.[70]

All these different organs of respiration[71] must act in

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essentially the same manner—namely, by absorption of oxygen (air) from the water by means of the osmotic action of their membranes. This action varies with the different animals. Bert[72] has shown that the powers of absorption even in nearly related species of fresh-water fish are remarkably various. Hence we need not be surprised to find that occasionally the amount of oxygen which is conveyed to the blood by the typical organs of respiration is not perfectly sufficient, so that the deficiency has to be made up in other ways. Nor are we more astonished to learn that the general respiration of the skin can be so increased that under some circumstances it suffices perfectly for the requirements of the animal, and renders the employment of the special organs of respiration quite superfluous.

The former case has been proved in Crustacea and in Fishes.

FIG. 50.—*Cobitis fossilis*. It swallows air-bubbles which pass through the intestine, where the mucous membrane takes up the oxygen for respiration.

Fritz Müller observed that crabs of various species (*Grapsus*, *Sesarma*, &c.) often raised the hinder portion of the cephalothorax, so as to let the air directly into the branchial cavity, as the amount of oxygen absorbed from the water through the gills was insufficient to supply their requirements. Many of our fresh-water fish, particularly all the species of Bleak (*Cyprinoidæ*), regularly swallow air in order to saturate the water that bathes their gills with oxygen, since the oxygen derived directly from the water is usually insufficient. The amount of oxygen needed by these fishes must be considerable, for it is much more easy to drown a fish than a frog if both are prevented from coming to the surface to swallow air; and yet the frog breathes by lungs, while the fish, on the contrary, is a true, gilled water-breather.[73]

An instance of the second case—*i.e.* that general respiration

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through the skin may perfectly supply the place of respiration through any special organ—is offered by frogs, which usually breathe through lungs. Milne-Edwards the elder showed long since that frogs, when prevented coming to the surface, were able to live under water so long as they were not cut off from the possibility of obtaining food and were freely supplied with fresh water. In such a case general skin respiration must necessarily take the place of lung respiration. Since then, Paul Bert [74] has shown that skin respiration can only take the place of lung respiration when, in the cold season, the temperature of the water varies between zero and 13° centigrade.

The instances here adduced prove at once that the absolute amount of oxygen needed for respiration and absorbed from the water varies according to the peculiarities of the different species, and perhaps even in individuals; and moreover that its absorption depends on certain external conditions, above all on the temperature. From this it further follows that there must be for every individual animal an optimum quantity of oxygen needed in a given time; if this optimum is not attainable by the ordinary organs of respiration, either the animal dies of suffocation, or else the deficiency must be supplied by some other means, as, for instance, in Milne-Edwards' experiment on the frog, by general skin respiration. To this category belongs too, in a certain sense, the air-bladder of fishes, which, according to the most recent investigations, may under some circumstances be regarded as an organ auxiliary to respiration. A body of gas is deposited in it from the blood which also contains oxygen, and this is rapidly used up if the fish is in water which holds but little oxygen. Now, although generally no air can be transmitted to the air-bladder from outside, still, as it would seem, it serves as a reservoir for the superabundance of oxygen which is introduced into the blood by the absorbent action of the gills and the skin. Very numerous experiments have been made on this matter, but they have yielded so many contradictory results that it is superfluous to go here into any closer discussion of them; and I refer those who are interested in the matter to Milne-Edwards' well-known work, 'Leçons d'Anatomie et de Physiologie comparée.' In a note [75] I have

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given the titles of some new works not mentioned by Milne-Edwards.

V. Power of enduring desiccation.—All water animals need a very high degree of moisture in the air or the direct contact of water to enable them to live; if a frog is transferred to dry air, it will quickly part with all its water to the atmosphere and perish of desiccation.

It has, however, been frequently stated of many water animals that they can endure perfect desiccation without dying. The experiments of Spallanzani, Dugès, Doyère, and others are generally known. Infusoria and certain worms of low type, the Rotatoria, the somewhat high-typed Tardigrada, and various kinds of Crustaceans, are said, according to these observers, to revive after being completely desiccated. The fact that when perfectly dry moss or hay is wetted all sorts of creatures are brought out of it is undoubted; but Pouchet's experiments account for this in a very simple manner, while, as it seems to me, they strikingly prove that true and complete desiccation infallibly destroys fully grown creatures. He showed that Infusoria, Rotatoria, and Tardigrada, when dried up in the nidus, always die if they are actually and truly desiccated, but that sometimes germs, or it may be eggs, contained in them, and which are protected from utter desiccation by their envelopes, on being moistened again develope rapidly, though still enclosed in the desiccated matrix, and creep out. These young animals creeping out from the eggs and germs have apparently been mistaken for the dried-up creatures resuscitated. The observations recorded as to the capability of many animals of the higher orders, even of Vertebrata, for enduring *drought* are not quite so erroneous; for it is not asserted that they themselves were desiccated. In tropical countries or in the Mediterranean province, where there is a sharp distinction between the wet and dry season, many animals fall during the latter into what is known as summer sleep. The *Protopterus* in Africa buries itself in mud, and surrounds itself with a thick perfectly desiccated crust, in which it is able to pass a latent life for months together, till the rain softens the crust and releases the fish. Many land snails attach themselves, during the day or

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during prolonged drought, to plants, stones, &c., or bury themselves in the soil and close the mouth of their shell with a calcareous deposit known as the diaphragm; thus they await the next rainy season to recommence an active life. Here it is easy to prove that the animals are not truly desiccated; for if we break into the shell of a snail thus found in its summer sleep, we see at once that the creature has preserved a very considerable amount of moisture, which the hygroscopically dry air has not been able to evaporate from the animal, protected as it is by its shell and diaphragm.

It is to this property possessed by living animals of retaining a certain amount, however small, of moisture for a long time in their tissues, and consequently of escaping total desiccation, that the power is evidently due which enables the eggs and germs of the above-mentioned animals to continue all the year round[76] in an apparently dry condition without being deprived of their vitality. It is certainly very striking that encysted Infusoria, and the ova or reproductive bodies of Crustaceans, Tardigrades, Worms, Sponges, &c., are capable of withstanding the long-continued desiccating effects of the air; but if at the same time we remember that it is extremely difficult to desiccate albuminous matter completely, even when dead, the fact loses something of its astonishing character. Living plants, too, often retain the last remnant of their moisture with much obstinacy.

Of the truth of these facts there certainly cannot be the smallest doubt. I have had for now six years a chest full of dried mud with the eggs of *Apus* and *Cypris*, which were sent to me in the spring of 1872 by Ehlers from Erlangen. Up to the present time every attempt to hatch out some of the Apus larvæ by softening a part of the mud has succeeded equally well in summer and in winter; the rapidity of their development is different, but this is due, as we have seen in a former chapter, to the degree of temperature at the time.

Now, remarkable as is this long resistance of eggs to drought, we are acquainted with a much more wonderful, and, in fact, hitherto inexplicable, fact connected with it. The eggs of various Crustaceans—as, for instance, of species of *Apus*—never develope[77] if they have not first lain some time in

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the dry mud. Living specimens of Apus caught by me in Würzburg deposited a large number of eggs in the water of my aquarium; not one developed. Mud full of eggs from the same pool from which I had taken the fully-grown Apus, after it had lain by for a full year, still yielded no larvæ on being wetted, and it was not till the second year that I obtained a few; but from that time I succeeded regularly in making them develope in great numbers, and whenever I chose. The statements of Brauer and others coincide with this. The eggs of the *Branchipus*, so nearly allied to *Apus*, do not share this peculiarity, but develope equally well whether they have been dried or kept constantly in damp mud. Brauer points out indeed, in his interesting notes on his experiments in breeding, that it would be very easy to rear animals of these groups from different parts of the world in our laboratories, and to study them at our convenience; since nothing would be needed but to obtain some dried mud from the localities where they live. In this way, for instance, Professor Claus was recently enabled carefully to investigate, in Vienna, the anatomy of the beautiful *Daphnia Atkinsoni* from Jerusalem. It would certainly be a grateful task to determine exactly what species of animals have eggs which can endure desiccation, or even absolutely require it, like Apus, to qualify them for development, and to find out also what the maximum period is during which they can endure to lie dry without injury to their vitality. A fundamental investigation of these questions would undoubtedly contribute much to a satisfactory explanation of many peculiar facts in the geographical distribution of the lower animals.[78]

Concluding remarks.—If we now compare the facts established in the different sections of this chapter with those previously ascertained, we obtain again the same general laws. Animals living in the same places, and apparently under the same external conditions of existence, nevertheless behave in quite different ways under the influence of the various substances held in solution in the water, as salt, oxygen, carbonic acid, &c. The ova of different and yet very closely related forms can endure a long period of drought, or even require it to enable them to develope. Hence every change, as, for in-

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stance, in the composition of the water of a lake or a river, will not affect the fauna inhabiting it equally and as a whole, but will act on individuals; some will bear the change without being in any way affected by it; others will die, while others again will survive, but their habits of life will be changed, and at the same time their structure will be modified, as in the case of *Branchipus* and *Artemia*. Thus the constancy of the aquatic fauna of any spot depends on the constancy of all the external conditions of life prevailing there, and every change, however small, in these will effect a selection among the old forms, facilitate the introduction of new ones, and sometimes even determine the transformation of one species into another. On this last and most important point we at present certainly know very little; but the old experiments of Beudant, the more recent ones of Plateau, and, above all, those of Schmankewitsch, show that this absence of information cannot be adduced as a convincing argument against the assumption that careful experiments directed to this question must tend to prove that stagnant water and the substances contained in it can exercise a far more direct transforming influence than has hitherto been considered possible.

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CHAPTER VI.

THE INFLUENCE OF A STILL ATMOSPHERE.

THE most important influence of stagnant air on the animals living in it is strikingly exhibited by those organs which are intended to respire air and convey it to the interior of the body. The physiological action of these air-breathing organs is exactly the same as that of the skin and gills in water-breathing animals. They bring the blood into the closest possible contact with the oxygenated medium. But as regards structure no greater contrast can be conceived of than that between the gills of a fish and the lungs (fig. 51) of the higher Vertebrata, or the tracheæ, as they are termed, of Insects, Myriapoda, and Arachnoidæ. These last (fig. 52) are usually fine tubes, with elastic walls with spiral thickening, which ramify in all directions, and which allow of the alternate inspiration of fresh air and expiration of foul air—charged, that is, with carbonic acid. This is effected by the opening and closing of the stigmata, or openings of the tubes, by the act of respiration, and by the expanding and contracting of the tubes themselves. These tracheæ thus convey the air, in extraordinarily fine particles, to all the organs,[79] so that their finest living portions certainly and abundantly absorb the oxygen they require direct from the air which is so brought to them. It is otherwise with the Vertebrata. Here the air is taken into sacs of a spongy structure (see fig. 51), of which the walls contain an excessively intricate network of blood-vessels; here, exactly as the skin or gills of fishes absorb oxygen from the water, the oxygen from the air passes by endosmosis through the mucous

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membrane of the lungs into the blood; this oxygenated blood is then carried to all the organs, of which the living portions take up the oxygen from it, precisely as the corresponding parts of insects take it up directly from the air by means of the tracheæ. In all animals that breathe thus through the lungs, there is a strongly marked contrast[80] in the blood contained in different parts of the vascular system. That which is carried back from the lungs to the heart is rich in oxygen and known as arterial blood, and that which circulates in the vessels which convey it from the organs to the heart, or from the heart to the lungs, is poor in oxygen, and is called venous blood.

We need not, however, in this place, investigate more closely the relations of the vascular system to the respiratory organs,

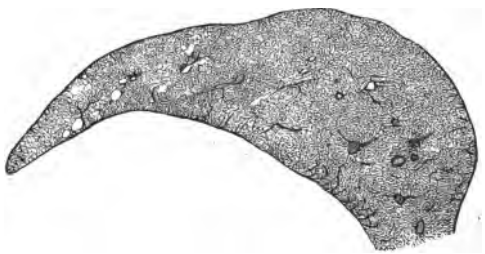

FIG. 51.—Section of the lung of the embryo of the Pig, showing the spongy texture.

nor the physiological distinctions which are based on the different organs of respiration and their structure. On the other hand, it is essential that we should in the first instance determine which of the constituents of the air are advantageous or injurious to animal life.

Air contains, when it is pure, almost 21 per cent. of oxygen, with about 79 per cent. of nitrogen, and a variable trace of carbonic acid, besides water which it holds in solution in the form of vapour in a quantity varying according to the temperature. All the other kinds of gas which are occasionally present in the atmosphere are of no importance. They are either irrespirable or actually injurious, while the above-mentioned mixture is the normal one, and thus is the most favourable for animal life. Certainly we must make this statement with

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some reservations; for, in the first place, we know that various animals are, as a rule, influenced in different ways by the medium in which they live; and besides, we cannot assert, on the basis of any experimental research, that certain gases which are injurious to men or to birds may not be indifferent or even

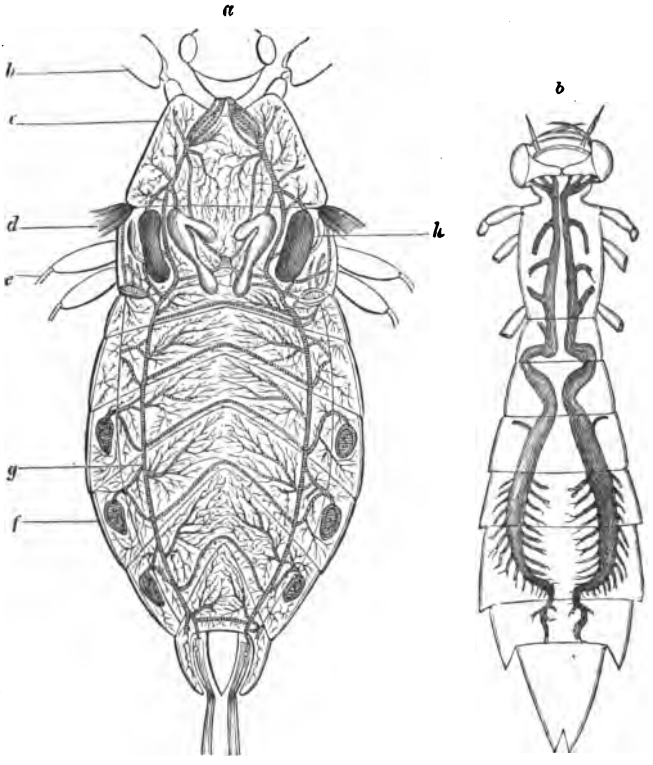

FIG. 52.—Tracheal system indicated within the outline *a* of a Water-bug, *b* of the larva of an Æschna. The tracheæ are shaded.

advantageous to other animals. For instance, it is well known that many larvæ of insects live in situations, as in decaying matter, where the air is undoubtedly mixed with gases which the higher Vertebrata could not breathe without injury; also that the capability for resisting the effects of irrespirable or

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poisonous gases is extremely different in different animals. Exhaustive experiments on this subject are not before us; hence the only general conclusion, as applicable to all animals, that we can draw from the experiments made on certain animals by physiologists, is, that every gas contained in the air affects the animals that breathe it according to its relative proportion, and to the peculiarities of each individual animal. Thus, for instance, carbonic acid, which is highly poisonous to man, ceases to be injurious when it is contained in the atmosphere in a proportion of only 1 to 2,000 (of volume); but even then it is not directly advantageous to animal life, unless, indeed, its stimulating action may perhaps be recognised as a not unimportant factor in the life of animals. At present, however, we know little on this point. On the other hand, we know positively that no air-breathing animal is capable of decomposing and assimilating carbonic acid as plants do;[81] nay, it may be doubted, as we have seen in a former chapter, whether even those aquatic animals — Sponges, Infusoria, Worms, &c.—which are said to have true chlorophyll in their tissues, do in fact make use of this constituent as an organ for the decomposition of carbonic acid; nor do we know whether the maximum of carbonic acid which can be endured by the few animals experimented on—which is perhaps even advantageous to some—is equally endurable by all air-breathing animals, or whether, for many of them, it may not lie even higher. Probably in this respect the various species, and perhaps even different individuals of the same species, may behave quite differently.[82]

What is of more importance to our enquiry, at any rate in this place, than the admixture of different gases in air, is the proportion of water contained in any given volume of air at a given time. Our personal experience teaches us that a dry or a damp wind has a totally different effect on different individuals; phthisical patients are sent in North America to the driest mountain regions of the Union, as Colorado, while in Europe they are frequently sent to very damp places, as Madeira, &c. Moisture in the air frequently induces rheumatism, but in this respect also different individuals are differently

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affected. We will now go more fully into a few particularly interesting cases of resistance to extreme dryness of the atmosphere, or to perfect saturation of the air with moisture.

I. The power of resistance to a dry atmosphere.—The atmosphere that lies near the surface of the earth is never perfectly dry; but we usually call it so when it is drier than is good for our health or agreeable to our feelings. This occurs, for instance, with tolerable regularity every summer in Würzburg;* many tropical regions are distinguished by a very dry climate; this is the case with the Sahara, the desert plains of Australia, and the desert coast of South America, where it never or very rarely rains; and even in tropical countries which are justly regarded as having a very damp climate—as Java or the Philippines—we nevertheless speak of a dry season, and everyone who has lived for any length of time in these islands knows that the dryness of the atmosphere there has a very unpleasant effect, although at least 50 per cent. of moisture is always present in the atmosphere. Hence all animals living in such localities must be able to withstand the desiccating effects of the atmosphere if they are to survive; and if an originally damp climate were suddenly, or even by gradual change through local disturbance or secular variation, to become a dry one, a great number of species would infallibly fall victims to this change in the conditions of existence.

Nevertheless animals live even in the driest places on the earth; many of these, indeed, belong to groups of animals of which the greater number require a very high degree of moisture in the air to enable them to live. This is the case, for instance, with many land Mollusca. Our common Road-snail and those Snails that creep about on trees require a very considerable amount of moisture in the atmosphere, or they cannot eat, digest, and grow. During the dry summer of the Mediterranean regions, even on islands, as the Balearic Isles, the active life and growth of these creatures is interrupted: they bury themselves deep in the dry earth or between slabs of

* The place where the Author writes; but the case is the same, of course, with many places on the Continent.

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rock, and close the opening of their shells with a lid (*operculum* or epiphragm)—often of many layers, and membranous or calcareous—which evidently contributes to prevent the utter desiccation of the creature. Other species again cling firmly to stones or plants, where they remain for weeks, and seem to be protected against the drought. Their powers of resistance, however, are not perfect; every collector knows that a certain number perish annually from desiccation, and these are by no means old and enfeebled individuals, which in any case were approaching the end of their life, but for the most part young ones, not fully grown. From this it would appear that the young individuals are less able to resist desiccation than older or fully grown specimens. The same phenomenon is observable in tropical regions with an insular climate; here the dry season generally affects the land-snails in the same way as in the Mediterranean province. Sometimes, however, local causes counteract the influence of the dry season. Thus, for instance, in a garden at Manilla in the Philippines, in the driest and coldest season, I found land-snails coupling, as well as their eggs and young, while in other spots the same or allied species were sunk in summer sleep. This was naturally the result of the increased local moisture of the air in this spot, under the thick leafy shade of large trees; nevertheless, even there, the absolute amount of vapour in the air was considerably less than during the wet season. Precisely analogous is the behaviour of Land-snails in deserts, where no one would expect to see animals living which part with the moisture from their bodies to a dry atmosphere so readily as snails do. These Desert-snails, as it appears, lead an active life only during the night or early in the morning, when a heavy dew moistens the soil; the moisture induced by the presence of vapour in the atmosphere is, however, very soon absorbed again, and during the dry day-hours the snails attach themselves somewhere where they are protected against desiccation. Thus the time during which they can imbibe the necessary moisture is about—or scarcely—as great for these animals as for the land-snails of the Philippines in the dry season. Still we must not overlook, in the first place, that probably they may be able to obtain a greater

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quantity of water from their food, consisting of the fleshy-leaved succulent desert-plants, than other snails; and, in the second place, that they may also be capable of absorbing a larger amount of water endosmotically through the skin than the snails living in our damp climates. Unfortunately, so far as I know, no experiments and observations exist as to the rapidity and period of growth of land-snails in countries where the moisture of the air differs widely or varies much. No series of systematic and accurate experiments are known to me, even with reference to our commonest snails, which collect in thousands every year, but only a few accidental observations;[83] so that the well-known statement of Agassiz—that in the shell of a *Helix* a ridge corresponds to each year's growth, like the annual ring in a tree—cannot at present be tested as to its general or partial accuracy. Researches in this direction would certainly be productive of results of universal value, as I am justified in concluding from a few general observations. Meanwhile from the few materials at hand as to the behaviour of land-snails under various degrees of moisture in the atmosphere, only one conclusion may be drawn which seems highly probable: That the various species behave very differently in this respect, so that an alteration in the moisture of the air in any region must fundamentally alter the Snail-fauna inhabiting it

Other animals perish from desiccation in quite other ways. For instance, in the tropics, as well as in North America, very many insects die out almost completely during the dry season, which by no means always corresponds with the hottest season, as it does in America. On the western side of Luzon, January, the driest month, is also the coldest. Certainly even at this season a number of insects are always to be found, chiefly individuals of the commoner species; but these are for the most part old and worn-out specimens, and it may be reasonably doubted whether they would live long enough to secure the permanence of the species by reproduction at the advent of the following damp, warm season in the month of May. This, on the contrary, probably takes place exclusively or principally by eggs which have been dormant during the dry season, as we may infer from the fact that immediately on

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the commencement of the wet season a multitude of young larvæ are to be found, which could not be the case if these old individuals had not till then coupled and laid eggs. Thus the eggs, though minute and only enclosed in a thin integument, show an especial resistance to drought. A parallel case is that of the eggs of many aquatic creatures which exhibit a power of enduring drought. I refer the reader on this point to what has been said above. But that the eggs of insects laid in the air, although perfectly protected by their envelopes, are not wholly impermeable to the air—that, on the contrary, they require that it should find access to the protoplasm of the ovum-cell—is proved by the following easily conducted experiment. If the eggs of insects are covered with a very thin film of resin or of oil, which prevents the passage of any air whatever through the pores of the integument, the embryos perish without exception, since the oxygen requisite for their respiration cannot penetrate to the protoplasm. Hence it follows that even though the ovum-cell may be partly protected against desiccation by the envelope surrounding it, yet the perfect immunity shown by the eggs of most insects must be partly due to the properties of living protoplasm.

II. The influence of a saturated atmosphere.—In many cases the moisture of the air reaches the maximum attainable under the existing temperature. This is not unfrequently the case, for instance, in European countries in the winter, and in the tropics during the rainy season, or under the leafy shade and protection of the primæval forests.

Unfortunately we know next to nothing as to the influence of such absolutely damp air on the animals living in it; we can only say that it is highly injurious to some, and to others again particularly advantageous. An extremely remarkable fact, depending on this, in the geographical distribution and habits of life of certain animals needs a closer discussion.

We should at first sight be naturally disposed to assume that species of animals whose organisation indicates adaptation to breathing water and to moving in water would be incapable of living in the air, since their skin must soon dry up in the air, so that it could no longer fulfil the functions proper

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to it, nor would they in many cases be in a position to use their organs of locomotion as such. The observed facts, however, do not correspond to this view, which was formerly somewhat hastily adopted. We know, on the contrary, that there are a tolerably large number of true aquatic animals which constantly or occasionally live on land. To these, for instance, belong the true Land-leeches, as they are called (fig. 53, *f*), which live in the forests of India and the Indian islands, sometimes in such enormous numbers that it is quite impossible for men to exist in them even for a few hours. I myself have often been driven out of the woods of Luzon and Mindanao, which are very favourable spots for insects and land-shells, by the myriads of leeches living on the trees and shrubs, from which they fall like a drop of dew on any human passer-by; and I once read that a whole English battalion had to beat a retreat during the Sikh rebellion because they were attacked in a wood by these small blood-suckers in such numbers that passing through the wood was not to be thought of. They dry up with particular facility; but as the air in these forests is constantly saturated with moisture, even in the driest season, they live in India in the open air on trees quite as well as their nearest allies, the Medicinal Leeches, do here in Europe in the water. Even more interesting are the land Planarians.[84] They breathe, like the leech, through the skin (fig. 53, *d*, *e*), and dry up even more readily; they move by means of fine, microscopically small hairs, the cilia or flagella, which are attached to the skin, and which by their peculiar motions can carry the animal forward when it is surrounded by a sufficient quantity of trickling water or of mucilage. On a perfectly dry surface, therefore, they cannot creep about for any length of time; the rapidly drying skin would soon yield up all the moisture which the cilia on the under side require for their motions. Hence these creatures are always found only in very damp spots; on rocks, however, as well as on trees, or even on the walls of houses. A few small land Planarians, two or three species, occur even in Europe, where they have already been found in Denmark, Germany, Spain, and France. *Planaria terrestris*, which was discovered at the end of the last century by

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O. F. Müller, was observed by me two years ago in the Balearic Islands—Minorca—where I found it under stones in a shady and very damp spot, far from all stagnant or running water.

Besides those just named there is still a considerable number

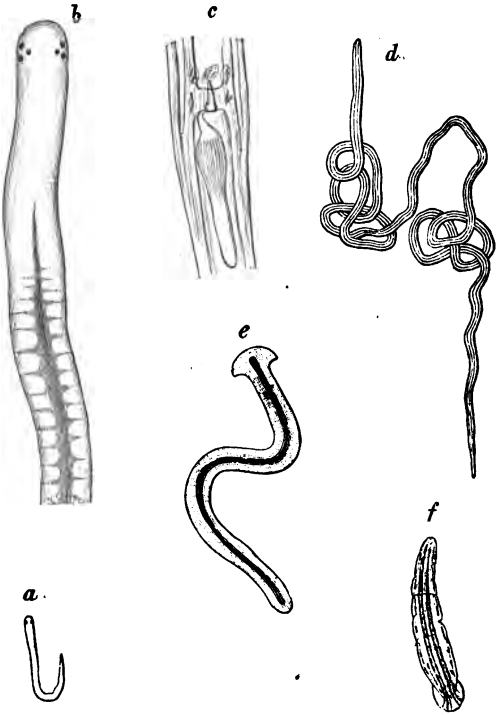

FIG. 53.—*a*, *Geonemertes palaensis*, a land Nemertean of the natural size; *b*, the head magnified; *c*, the proboscis and spine, with the poison-gland of the same creature; *d*. *Dolichoplana striata* (Moseley); *e*, *Bipalium* sp., both land Planarians from the Philippines; *f*, Land-leech from the Philippines.

of aquatic animals that live normally on land. To the land Nemertean discovered by me in the Pelew Islands of the Pacific Ocean (*Geonemertes palaensis*, fig. 53, *a*—*c*) a second has been added by Von Willemoes-Suhm; they live with land Planarians under stones or low-growing plants.[85] Many crabs of the

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family of *Orchestidæ* (fig. 54) live exclusively on land, although they have the gills proper to all aquatic species. In the summer of 1876 I found in Minorca an enormous number of individuals of one species [86] under large stones in the perfectly dry bed of a stream, during the driest season of the year; and in the islands of the Indian Archipelago they are often quite as frequent as the Land-leeches in damp and constantly shady woods. Various species of *Neritina* [87] frequently occur on dry land far from any water; other species live constantly or during the chief part of the year high up on trees in mangrove swamps—groups of *Neritina dubia* and *N. ziczac*.

In most of the cases here adduced, the organisation of the animal appears, so far as we know, to be entirely that of a creature living and breathing in water, or only very slightly

FIG. 54.—*Talitrus saltator*.

modified. The Orchestidæ, Nemertidæ, Snails, and Leeches show not the smallest difference from their nearest allies living in water; in the land Planarians, however, a creeping surface has developed on the under side, which acts physiologically in the same way as the foot of the land snails, and which is not found in Planarians living in water. But undoubtedly there are, among Fishes and Crabs (*Brachyura*) for instance, many forms which constantly, or only occasionally, live on land in damp spots, and have undergone a more or less considerable transformation, particularly in their organs of respiration. As these cases are of more general significance, we will investigate them somewhat more in detail.

III. The accommodation of water-breathers to breathing air.—Fish, as is well known, breathe through their gills, which, being set at the sides of the head and covered by the operculum,

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absorb oxygen from a current of water which enters by the mouth, bathes the gills, and passes out again behind the operculum through the gill-opening. Hence fishes would appear to be confined exclusively to a life in the water. Nevertheless there are a few forms which are able to breathe out of water, and which in fact even pass a great part of their lives out of water. Such are the two genera, both belonging to the Gobiidæ, *Periophthalmus* and *Boleophthalmus*; these skip along close to the water-line on the sea-shore, where they hunt for Molluscs (*Onchidium*) and Insects. In their branchial cavity, like all fishes, they have true gills; but these, though not differing widely from those of other fishes living constantly in the water, are far from filling up the cavity, which is rather large; and this seems to contain not merely water, but air as well. In other fishes that occasionally visit land, the branchial cavity on each side is prolonged, and penetrates upwards far into the head, while its mucous membrane sometimes forms labyrinthine folds of highly complicated structure (see fig. 47); hence their surface is often much more extensive than that of the true gills. Formerly the species which possess this accessory labyrinthine organ in the gill-cavity were classed in one family of *Labyrinthici*, for it was thought that their internal affinities were clearly denoted by the presence of this organ. Now, on the contrary, they are distributed into several different families,[88] since it is considered as proved that their real genealogical affinity is indicated by other characters, while the labyrinthine organ must have originated independently in certain forms of these different families, though with great similarity of structure and identical physiological functions. Formerly this function was explained by the hypothesis that water could be stored in the cavity of the labyrinthine organ, which might be closed, and that this water, being rich in oxygen, and unable to escape from the gill-cavity, enabled the creature during its excursions on land still to breathe in or through water. There can be no doubt, since numerous observations exist on this point, that they are capable of living for days out of water; many of them make long journeys over land, and some are even said to be able, by means of the spines on their scales and gill-

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covers, to climb up palm-trees—*Anabas scandens*. I have certainly never seen this, though I have often caught *Anabas scandens* in the Philippines. But the hypothesis that their labyrinthine organs are merely auxiliary gills destined to enable the fish still to breathe through water when on land, finds no confirmation in the observations made by the most esteemed naturalists; indeed, it is quite incomprehensible how, in so minute an amount of water as could find place within the labyrinthine organ, so much oxygen could exist as the creature must consume even in a few hours. And there can be no possibility of a renewal of the water deprived of its oxygen so long as the animals live on land. It is, however, at this day, almost superfluous to point out the absurdity of this early and often disputed assumption by an analysis of the physiological processes; for the direct observations of Dr. Francis Day [89]—known by his great work on the fishes of Malabar—have proved that the accessory gill-cavities, or labyrinthine organs, as they were called, of the Labyrinthici never contain water, but always air only. So that these organs must be simply designated as organs for respiring air, *i.e.* as lungs which have been formed by modification of a portion of the water-breathing gill-cavity; the fishes that have them are therefore to be regarded as Amphibians with quite as much reason as toads and frogs, or even better, since they are capable of changing the nature of their respiration—of air, that is, or of water—at will and suddenly without any interruption; nay, are actually accustomed so to change it. Finally, in some Brazilian fishes—*Sudis gigas*, *Erythrinus tæniatus* and *brasiliensis*—the air-bladder, as Jobert has lately discovered, serves directly as lungs subsidiary to the gills, since they inhale air through a connecting passage which subsists between the throat and the air-bladder. If this air-passage (*ductus pneumaticus*) is ligatured, the fishes die of suffocation, since the amount of air obtained through the gills does not suffice them for respiration. By these observations it is made intelligible how an air-bladder could be transformed into a lung. Insufficient absorption through the gills brought the fish to swallowing air; instead of passing out through the gill-openings, as in other fresh-water fishes, the air passed into

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the intestine or even into the air-duct leading to the air-bladder, and thus both organs might become organs of respiration, since, fundamentally, every growing or living cell must breathe as soon as it comes into contact with a highly oxygenated medium.

Even among the Invertebrata we know of animals which may, in this sense, be designated as true Amphibians. The opercu-

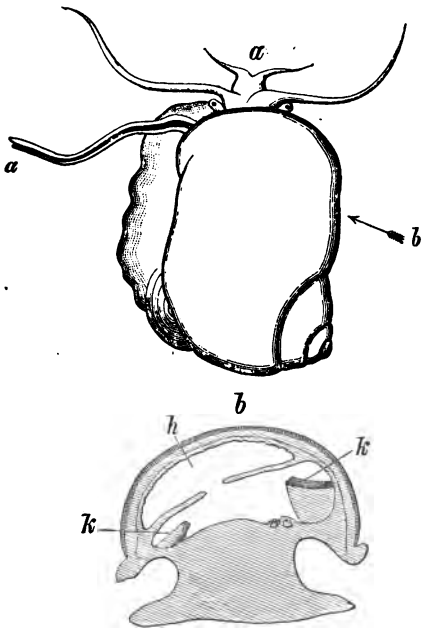

FIG. 55.—Gill-lungs of Ampullaria. *a*, *Ampullaria insularum* (D'Orb.). *a*, long respiratory siphon; *b*, section in the direction of the arrow *b*; *h*, the upper lung-cavity; *k*, branchial cavity with the right and left gills; the cavities communicate by a passage in the centre of the dividing wall.

lated snail *Ampullaria* (fig. 55) has a well-developed branchial cavity and gills, and above these, and separated from them, it has a well-developed lung-cavity, of which the structure is precisely similar to that of the lungs of our common land-snails. The Ampullaria uses both organs in rapid alternation; lying not far from the surface of the water, it protrudes above it a breathing siphon, and inhales air through it; then it closes its

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lungs, reopens the siphon, and admits a stream of water through it into the branchial cavity.[90] Some species of *Neritina* of the Philippine and Pelew Islands live constantly on land, and apparently go into the water only when they want to lay their eggs; other species actually living in the water often make long journeys over land, as I myself have frequently had the opportunity of observing in the Pelew Islands. In these species the gills are comparatively small, and the roof of the branchial cavity is furnished with a dense vascular network of which the main branches unite in one large vessel; this is inserted in the heart—the auricle—and thus stands in precisely the same relation to the lungs as the pulmonary vein of the true

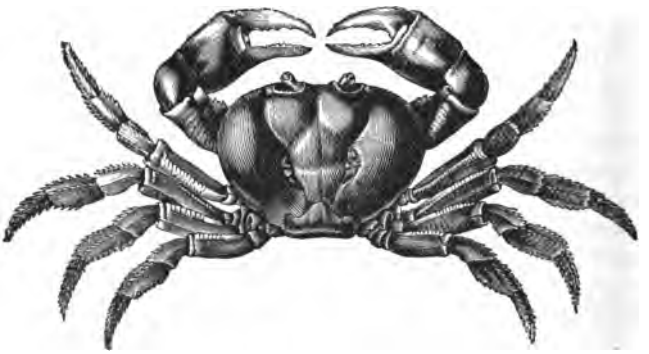

FIG. 56.—*Gecarcinus rusticola*, a Land Crab.

land-snails—*Helicidæ*. Thus the branchial cavity in this case seems to be capable of fulfilling not only its own proper functions, but also that of a lung. We know, moreover,[91] that many species of crabs—*Birgus latro*, *Gecarcinus* (fig. 56), *Grapsoidea*, *Sesarma*, and others—live far from all running or stagnant water in damp woods, under stones or decaying trees, and are even able to expose themselves to the sun for hours. In most of these species true gills are present in the branchial cavity, but they fill at most a third or fourth of the space, and the cavities contain, besides water, a considerable quantity of air, as is shown by their constantly expelling air-bubbles at the sides. The supply of air thus driven out can of course be

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replaced only by air, since the animals live in the air, and it obviously follows that they generally breathe air with their branchial cavities, and only exceptionally water.[92] In one single case this change of function has induced a modification of structure; this case is that of *Birgus latro*, according to my own observations. The lower portion (see fig. 2, p. 5) of the gill-cavity, which contains numerous but small gills, is divided from the upper half by a transverse fold which turns inwards at the edge of the thorax-plate. The cavity thus enclosed is a true lung (see fig. 2), since it never contains anything but air, and the arrangement of the vessels traversing its walls proves that blood poor in oxygen enters it from the body, and the vessels leading from it open directly into the auricle. The skin on the outer and upper lung-covering bears a great number of ramified tufts, which add to the extent of the respiratory surface, and contain in their interior an extraordinarily developed network of vascular spaces, intervening between the afferent and efferent pulmonary vessels. These spring from two large vessels, proceeding one on each side from the anterior half of the body cavity; each divides close to the foremost angle of the lung into four pulmonary vessels, of which three ramify over the upper and one over the lower lung-covering. These are merged in the before-mentioned network which traverses the villi of the lungs. From this again proceed several vessels which unite at the angle of the lung to form a large trunk, the afferent pulmonary vessel; this passes at first from the front backwards, then bends round, corresponding to the curve of the thorax-shield, and passes from behind forwards, uniting with the branchial vein coming from the interior, shortly before it enters the auricle of the heart. This arrangement of the vessels is such as we should expect to find in a true lung; the expansion of the respiratory surface which is here afforded by the villous structure of the lungs equally corresponds to the typical structure of all organs for breathing air; finally, it is positively established that the animals pass the greater portion of their life on land, and that their lung-cavities contain actually air, and never water in any greater quantity than is requisite for maintaining the moisture of the respiratory surface.

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Now, since this lung perfectly corresponds, morphologically, to the upper half of the branchial cavity of other crabs, proof is furnished that here a portion of the gill-cavity has been transformed into an organ for breathing air, and has at the same time undergone very characteristic modifications of structure.

The objection which certain morphologists feel to admitting that land crabs, and above all *Birgus latro*, are animals actually breathing air and provided with lungs, appears to be caused by their incapacity for understanding that the same organ which to-day acts as a lung may be used to-morrow as an organ for breathing water by the employment of the gills placed in it, or close to it. This objection is all the more to be wondered at, since the same zoologists readily admit that this same process—the transformation of a gill-cavity into a lung—has actually taken place in snails. The lung of Ampullaria spoken of above might be here adduced; still it might perhaps be said that it is not proved that it belongs morphologically to the branchial cavity, and that it may be a new organ occurring only in this genus. But the same objection could not be made with regard to the lungs of the Helicinidæ, Cyclostomaceæ, Siphonariadæ, and hermaphrodite Pulmonata, for all these Molluscs have only one respiratory cavity, which breathes air, but which, by reason of its position and its relation to the other organs, may be regarded as a gill-cavity transformed into a lung, and which is even regarded as such by all zoologists. But there are among them certain forms—*Siphonaria*, the aquatic Pulmonata, *Auricula*—which bear a small gill or gill-like organ in this lung, notwithstanding that it is filled with air; consequently even those zoologists who dispute the air-breathing powers of *Birgus latro*, merely because it possesses gills, must regard the above-mentioned molluscs as water-breathers also. This, however, they do not do, for they cannot deny the fact that these creatures breathe air; hence they will be obliged by degrees to accustom themselves to the idea that land-crabs breathe air, and to regard the lungs, in them as well as in the snails, as gill-cavities which have exchanged their normal or primary function for another.

At the first glance it certainly appears singular that an

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aquatic animal whose organs of respiration are adapted to breathe water should be capable of learning to breathe air with them. If, however, we enquire somewhat more closely into the character of the process, it loses much of its strangeness. In both cases the oxygen is absorbed from the surrounding medium by a membrane which is kept moist, and to which it must be a matter of indifference whether it receives it from air or from water. Thus, granting that in both cases the osmotic power of the respiratory skin remains the same, as the amount of oxygen taken up within a given time naturally depends on the proportion of oxygen contained in equal determined volumes of the air or of the water, the respiratory surface may be in a position to take up more oxygen from the air than from the water in the same unit of time, because air has a larger admixture of free oxygen. Thus—if there is no other hindrance to an alteration in the mode of life—on the above hypothesis, an animal, which has hitherto breathed in water, will more easily accustom itself to breathe in air than an animal living in the air, on the contrary, can accommodate itself to breathing in the water; for in this latter case a deficiency, which must inevitably arise, must first be covered by auxiliary organs—by the skin, for instance—while in the former the originally small requirements of the water-breathing animal will be much more easily supplied by accommodation to the more copious respiration of air than by its continuing to breathe in water. But whether the creature is, without exception, benefited by a change of function, by which a medium poor in oxygen is exchanged for one rich in that element, of course is not proved; while, on the other hand, it cannot be disputed that some such advantage may be connected with it.[93]

The causes which prompt an animal to quit the water and to accustom itself to breathe air may be of very various natures; lack of food, need of shelter, and the pursuit of prey or flight from foes most likely play the most important part. It is, however, also possible that other causes which are less obvious may have led to the same result; thus, for instance, the absolute deficiency of air in the water under some circumstances may undoubtedly have exerted this influence. When

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river cray-fish are kept in stagnant water, they soon die for want of oxygen, or else they quit it and prefer to live in the air; it is well known that they are packed for carriage in wet moss, and not in water. Further back I have already mentioned (see p. 172) that fishes are easily drowned if they are prevented supplementing the amount of air they derive from the water, which is insufficient for their respiration, by swallowing air at the surface. Fritz Müller has made us acquainted

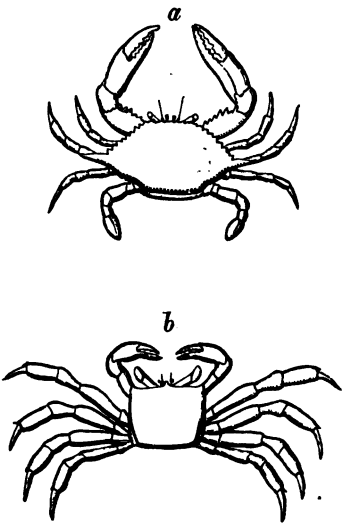

FIG. 57.—*a*, *Lupea*, a swimming crab that breathes only in water; *b*, *Ocypoda*, a marine crab which easily suffocates in water.

with a few other examples. He showed that the *Ocypoda*, which lives half its time on land and in part breathes air (fig. 57, *b*), can easily be drowned if it is held in sea-water, which yet contains enough oxygen to allow a *Lupea diacantha* to recover itself perfectly when it has been almost killed by being kept in the air. It follows from this that the osmotic power of the respiratory dermal surface is extremely different in the two animals, and that in the *Ocypoda* it is not great enough to extract the considerable amount of oxygen necessary to the

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creature from sea-water, which contains but little air, in the same time as from the air directly. The *Lupea*, on the other hand, cannot breathe in the air; perhaps for this reason, that its gills completely fill the cavity, and so the ingress of air is hindered by the gill-laminæ which lie too close together; most fishes die quickly in the air in the same way and for the same reason, because their gills collapse and the respiratory surface is conspicuously diminished.

It is, however, only an hypothesis when we speak, as above, of a transformation of the gill-cavity into a lung; for in none of these cases have we ourselves observed the process or attempted hitherto to induce it by experiment; nay, we do not even know whether Crustaceans living on land, and breathing air—as, for instance, *Birgus latro* or *Gecarcinus*—fill their lungs with water and breathe through water, when in the water, or breathe exclusively through their gills so long as they are under water. From the morphologist's point of view, however, this hypothesis may be regarded as satisfactory; for, in the first place, the structure of a gill-lung is precisely such as we should ascribe to an organ for breathing air, and, in the second place, its position in the body is such that its derivation from the gill-cavity or from some portion of it is immediately apparent.

Moreover, and finally, there is another instance that has long been known of such a transformation of a branchial cavity into a lung, but whose full significance has only quite lately been duly estimated. The Limnæidæ, living in fresh water, have true lungs; they go from time to time to the surface of the water to take air into these lungs, and the oxygen contained in it suffices for some time as supplementary to that which they absorb through the skin. Now it has long been known that the lung-cavity of the young Limnææ when they escape from the egg is full of water, and it apparently acts as a gill-cavity so long as the animals do not find their way to the surface of the water to inhale air into the gill-cavity and thus transform this into a lung. Generally, it is true, this period of water-breathing through gills is not of very long duration, perhaps of only a few hours; but Professor Forel, of Lausanne, has made us acquainted with some experiments which prove that there are actually

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Limnæidæ which breathe water throughout their lives. In the course of his investigations of the deep-water fauna of the Lake of Geneva, he brought up from a depth of 130 fathoms, among other animals, some Limnææ which had in their lungs no air, but only water, and which lived there in great numbers and at various ages and stages of growth. But as soon as the creatures brought up by the drag-net were transferred to a small vessel with water in it, both old and young soon crawled to the surface, opened the orifice of their lungs, and inhaled air into the respiratory cavity, which was still filled with water, and with which, till within a few moments, they had breathed only water all their lives. This incontrovertibly proves that an organ of respiration may be able to alter its function, not only gradually but quite suddenly, and the apparent contrast between air and water breathing consequently loses much of the significance hitherto ascribed to it. On the contrary, every water-breathing organ can easily be brought to breathe in the air, if only two conditions are fulfilled: First, the maintenance of moisture in the respiratory surface by the condensation of the water contained in the atmosphere; and, secondly, the prevention of the collapse of the organ, and the consequent diminution of the respiratory surface.

These observations accidentally made by Forel have given rise to a very interesting experimental treatment of the question by Dr. Pauly. He showed that the Limnæidæ that exist in the depths of various lakes, of Geneva, Constance, and Starnberg, where they can never come to the surface to breathe, can live by respiration through the skin and by using their lungs as gills; but according to Pauly the chief action is to be attributed to the former. He further found that they frequently contained air in their lung-cavities without coming to the surface of the water, and that they obtained it by taking the numerous air-bubbles that cling to water-plants or stones into the respiratory orifice. Finally he proved by experiment that a Limnæa from deep water, which had for the first time become accustomed to breathe air, never returned to water-breathing; on the contrary, it kept its respiratory cavity completely closed, and breathed subsequently by the skin alone while under water.[94]

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Concluding remarks.—With regard to the selective influence of air and of the matters held in it—oxygen, water, carbonic acid, &c.—the same general conclusion may evidently again be drawn as we arrived at in the former chapters; it results from the fact that different animals or even individuals never react in precisely the same way under the influences of the atmosphere. Every change in its composition must therefore essentially alter the fauna of a country or of a locality by selection, if this change is not merely a transitory one—in which case an injurious or favourable influence may find compensation—but is continuous for a lengthened period. A conflict between the individuals thus affected need no more take place under the selection caused by the conditions we have now been investigating than under any we have hitherto discussed. Such a struggle can arise from this cause only when, from a superabundance of animals, the quantity of air at their disposal for respiration has to be so greatly subdivided, that it fails to be equally favourable to all the individuals. But while in all the former chapters we recognised not selective effects only, but also with more or less success a direct transforming influence as exerted by the conditions under discussion, and even could sometimes experimentally prove their existence, this has not been the case as to air. The proof that a change in the function of respiration is possible may indeed be acquired by experiment, and a not insignificant number of differences in the structure of the respiratory organs concerned may be very naturally conceived of as an immediate consequence of such a change of function; but in no single case have we as yet succeeded in proving that such a change of function as is involved in the transformation of a gill-cavity into a lung must necessarily be accompanied by definite changes in the structure of that organ. Still it must not be forgotten that in this respect we are not yet past the stage of the most superficial and elementary knowledge.

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CHAPTER VII.

THE INFLUENCE OF WATER IN MOTION

In the previous chapter we saw that the distribution of animals on our globe would be essentially modified by a change in the proportions or in the chemical composition of air or of water. If the air were deprived of the greater part of its oxygen, only a very few species of animals could continue to live—only those, that is to say, which could endure such a diminution of the respirable oxygen contained in the air. If, on the other hand, a larger quantity of oxygen could be added to the water than it usually contains, it would appear probable that many animals fitted for breathing in the air would be thus enabled to live in the water if any other cause made such a change of habit inevitable; consequently land animals would become aquatic. It is not probable that such a complete change could now ever actually take place; but smaller changes in those conditions of life might occur, in fact actually do occur. We know, for instance, that, according to the direction of the wind, the air at the surface of the earth is light or heavy, that it is of different density in low plains and on heights, and varies very greatly in its composition; it is different in the dwelling-places of man and under the shady roof of forest trees, on the open sea and in the Sahara or the boreal regions of the eastern and western hemispheres; and the percentage of moisture in the air varies with the temperature and the prevailing winds. The constituents of water are equally variable; in lakes with marshy shores they are not the same as in running brooks or rivers; they are different on a limestone soil and on sandstone; the amount of saline matter in solution (*sensu strictiori*) varies con-

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spicuously in the different oceans and inland seas; some water is rich in oxygen or carbonic acid, in others these are wanting; in some cases we find large quantities of calcic carbonate, magnesic sulphate, and other salts in the water, which is then termed hard; in others, as is usually the case with rain-water, these salts are almost entirely absent.

All the differences here briefly enumerated, and many others not specified, which affect those conditions of existence which depend on air and water, must have more or less influence on the forms of animal life; some species will absolutely die out, others will remain wholly unaffected, while others again will become modified in their habits of life as well as in the structural relations of their organs (for instance, *Branchipus* and *Artemia*). Now, if we assume that these variations must be perfectly inappreciable to our individual perceptions—secular variations, as they are termed—the modifications which are caused by these secular variations in the animal life of any given country must also be inappreciable by man; the apparent constancy of the conditions of life, so far as they depend on air and water, will make the fauna appear equally constant to our unaided vision. This hypothetical constancy does actually exist, if we disregard the variations occurring within the space of a day, a month, or a year; the salt constituents of the different oceans and inland seas remain perfectly identical, as well as the moisture contained in the air or in the composition of the atmosphere; we are in no way cognisant of any perceptible variations in the conditions of existence within the historical epoch of our globe. Hence we may without hesitation assume that any alteration caused by such variations in the fauna of any locality or in the mode of life of any animal and in the structure of its organs can never have been perceptible to us.

Nevertheless these two conditions of existence, air and water, are precisely those which are most constantly at work on animal types, and which are also the best qualified of any to bring them into ever fluctuating conditions of existence, and it is their capability for being moved of which nature avails herself to effect the constant transfer of animals from one

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place to another. The passive migrations of animals are effected entirely by the winds or currents, and their voluntary movements are limited or favoured by them. Finally, the strength and direction of these currents in the air and water provide nature with so many instruments for influencing different animals in their individual life and growth; among those so influenced, above all, are those which we may call sedentary, in which a marked effect on the mode and vigour of their growth can be traced to the moving medium.

We will begin our enquiry into these important problems by investigating the influences of *water in motion*. But it must once more be pointed out that the influences discussed in our former chapters must always be inseparable from those proper to the currents, so that the total effect of the water arises from the combination of several influences, not one of which need ever act in the same direction as any other; on the contrary, they frequently neutralise each other. If, for instance, the larvæ swimming in a sea were, without exception, drifted by the same current simultaneously into an estuary, they would apparently be thus enabled to take possession of the new territory; nevertheless all those forms would die out which were not at once able to endure the reduced saltness of the water in the estuary. A stream of warmer water, as, for instance, the Mozambique Channel flowing past the east coast of Africa, will have a tendency to convey animals of warm latitudes into the colder seas; but only a few species—those we have designated as Eurythermal—will be able to establish themselves in them easily. It is true that the difference in the conditions of life under migration by means of sea-currents is not always so conspicuous as in these extreme cases; but all creatures are exposed to changes of less intensity, if, in the larva or in the fully grown stage, they are borne from one place to another.

If we now leave out of the question those influences of the constituents and temperature of the water which are inseparable from its currents, and direct our attention solely to these, the mechanical factor of their momentum is what we have to consider as exclusively important. The direction, the rapidity, and the strength of the current unite to affect the animals

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exposed to them; some they will annihilate, others they will transport against their will to other spots, and others again they will affect by hindering or promoting their growth.

The resistance of animals to currents.—The effects of water in motion may be displayed in two different ways: in the first place, as sudden and irregular blows, as in the beating of waves or surf; secondly, equally and uninterruptedly, as in currents. Excepting in some few instances, we need not enquire more closely into the effects of sudden shocks, for either they at once destroy the creatures exposed to them, or these are able to withstand them; this, however, can but rarely be the case under heavy blows. Currents are far more important.

In general we estimate the pressure of a current, in seas, rivers, or torrents, by its velocity, assuming that the current exerts its force perpendicularly to the body resisting it. Such

FIG. 58.—Mollusca that cling tightly to rocks by the foot. *a*, *Patella*, the shell of which entirely covers the soft parts, which are pressed down on the rock; *b*, *Navicella*, fully extended, only the tentacles projecting beyond the front of the shell.

cases, however, but rarely occur in nature, and in places where a current or high waves break perpendicularly to the cliff a very small number of animals can live—such, for instance, as are sufficiently protected by the strength and form of their shells against destruction, or by the sucking power of their foot against being torn or washed away, like *Patella* in the sea (fig. 58) or *Navicella*[95] in strong mountain torrents; or forms which not only are covered by a hard external shell, but whose shell is grown to the rock, such as the Sea-acorns (*Balanidæ*). The pressure to which these animals are subjected, either perpendicular or lateral, must sometimes be enormous; it would be interesting to ascertain by experiment how great it actually is in individual cases. A knowledge, however, of the maximum of pressure which can be generally borne by the animals above mentioned and others of analogous

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structure, would not, as it would seem, be of any universal interest; for it must be very difficult, if not actually impossible, to make experiments on such creatures. We must remain satisfied with the fact that permanently fixed animals, or such as can attach themselves temporarily, exhibit, without exception, organs of such structure, form, and character as most clearly prove the adaptation of the animal to the development of its powers of resistance. Their fitness to live depends exclusively on this power of becoming fixed or of clinging; and if once they are displaced by a too violent lateral shock, death almost always ensues.

This group of sedentary animals, spending their lives fixed to one spot, exposed to and resisting the pressure of water in motion, may be contrasted with another which, to express myself for once in the terms of the Teleologist, so far overcome the momentum of the water as to use it to their own profit. Swimming animals do not feel the strength of the current so long as they swim with it or are carried on by it; it is only when they try to swim against it, directly or at an angle, that they feel its force, and it is not till then that they develope those organs or characters from which they derive the requisite power of resistance. It is perfectly immaterial to all the very tender sea creatures, containing not more than from two to three per cent. of dry matter—such as Siphonophora, Medusæ, Salpæ, and larvæ of all kind—whether they are carried by the current at a rate of two or of ten miles an hour; nor, indeed, can they be conscious of it so long as they are not flung against a hard object.

We will consider these two groups, and the organs which distinguish and demarcate them, somewhat more closely.

The organs and characters which are possessed by migratory animals, and allow of their moving and of their taking advantage of the transporting power of the currents, are extraordinarily various; and yet they admit of our easily dividing the animals into two great groups. These are (*a*) the animals that move voluntarily or swim, and that move from place to place of their own free will; and (*b*) those that move involuntarily or float and are carried passively by the stream. The former require

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swimming organs, the latter do not. In the former the specific gravity, compared with that of the stratum of water in which they live, must be a little in excess. In the latter it may be the same as that of the water, or even less. This comparison, however, is not, and cannot be, absolute; for since the strength of the current varies with that of the wind, with the fall and the mass of water, &c., most of the actively swimming animals even, must often be transported passively, as, for instance, when their strength is insufficient to contend with the current; nay, even the strongest swimmers, as the Porpoises, Whales, Sharks, &c., must often voluntarily allow themselves to be borne along by it. Those organs which serve to enable swimming or floating creatures to maintain a position at the surface or at a certain level, are known in zoology as hydrostatic organs; to these belong, for instance, the swim-bladders of many fishes, the air-bladders which keep floating colonies of polyps (*Siphonophora*) at the surface of the sea,[96] also those air-vacuoles which are sometimes found in the protoplasm of testaceous Rhizopoda (*Arcella*). Even creeping animals, such as the fresh-water snails (*Limnæa, Physa, Planorbis*, &c.), can become floaters, for they fill their lungs so full of air that they become specifically lighter than the water, and consequently rise to the surface.[97] This enables them to creep by the motion of the cilia or by the action of the foot on the stratum of air in contact with the surface of the water. It is easy to see from these examples that nature employs an infinite variety of means for solving so simple a problem. In *Arcella* it is a temporary bubble, which disappears when the creature desires to sink to the bottom; in the Siphonophora the organ appears to serve no purpose but that of keeping the colony at the surface; in Fishes, as we have seen above, the hydrostatic organ also subserves the purpose of an air reservoir, and in some cases even of a lung in the physiological sense; in the pulmonate water-snails, again, the lung itself can, at the will of the animal, become a hydrostatic organ.

Far more various and important are the actual swimming organs of the true swimmers, by which they are enabled to exchange an unfavourable spot for one more suitable, to escape the pursuit of their enemies, or to extend their own hunting-

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ground. In the first place, in all swimmers, the whole body serves as a means of motion; snakes and eels or similar creatures with very long bodies swim exclusively or in preference by a wriggling motion, and even much shorter animals, as bleak, &c., can swim without fins, but then their power of directing their movements is greatly impaired. Such organs as

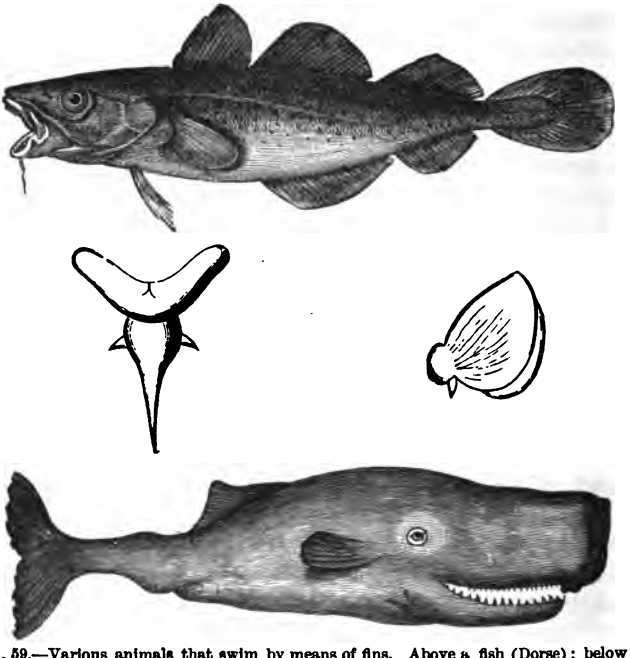

FIG. 59.—Various animals that swim by means of fins. Above a fish (Dorse); below a Cachalot Whale; to the right a Pteropod, *Hyalea*; left, a Pteropodous larva (*Creseis?*).

serve exclusively or chiefly to enable swimming animals to move in a determined direction are known by the general term of fins. Notwithstanding the widest difference in their structure, and though they may have but small morphological correspondence in different creatures—as will be understood, without any more detailed comparison, from the subjoined illustration (fig. 59)—they have, without exception, certain peculiar characters, which

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have a direct reference to their purpose and function. In the first place, they have cutting edges and a broad surface, by which the animal is enabled to exert pressure on the water in the most efficient and natural manner; in the second place, they are, without exception, attached by movable joints in such a way as to serve for steering. Such fins occur in the greatest variety in both Vertebrate and Invertebrate animals; in whales, sea-serpents, and tailed Amphibia, on the tail; in many Fishes, as single fins on the back, belly, and tail, and as paired fins on the body, where the lower or hinder extremities or limbs are modified into fins. In many Birds, both wings and legs serve as fins;[98] Mammalia and Reptiles alike are often fin- or web-footed (crocodiles, turtles, and aquatic mammalia). In insects, the legs (in *Notonecta*) and sometimes special appendages of the body (as in the larvæ of *Ephemera*) or even the wings (*Polynema*), are used for swimming; in many Crustaceans all the legs are true fins, and in several of the Annelida each segment of the body bears a pair of fins. The larvæ of Mollusca have them on the head, Cuttle-fish at the hinder end of the abdomen; in short, there is hardly any portion of the body on which some little lobe or process might not serve as a fin. A small and delicate creature, like a Medusa or the larva of a Mollusc, may find a ciliated disc or margin, or even a few scattered cilia, efficient as fins in spite of their fragility; large animals, as whales, sharks, &c., require larger fins provided with strong muscles, and supported on an internal skeleton. In all cases the serviceableness of these organs depends on their being fitted to move the whole mass of the creature in a definite direction, with or against currents; if the extent of surface of the fins, or the strength of their motor muscles, or the supporting power of the skeleton, is insufficient for this purpose, the individual possessing such inefficient fins must necessarily perish. Thousands or millions of such inefficiently equipped aquatic animals must be swept away every day and every hour by the currents to which they are forced to commit themselves, and here again the external conditions of existence select the stronger, and eliminate the weaker, individuals, without the need of any personal struggle between them.

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Sedentary animals, not properly swimmers, are either fixed to their dwelling-place or only temporarily attached. The way in which these animals either yield to or overcome the effects of currents has already been indicated; the hardness and shape of the shells, the adhering power of the foot, or of the skeleton—as in corals—protect them against the steady lateral pressure of currents, but if they lose their hold or are broken off, they are soon destroyed. Only certain creatures, as many sponges and some polyps (*Hydroida*), although they are fixed, escape by other means the destructive effects of strong currents; their extreme tenacity of texture, elasticity, and pliancy, in which

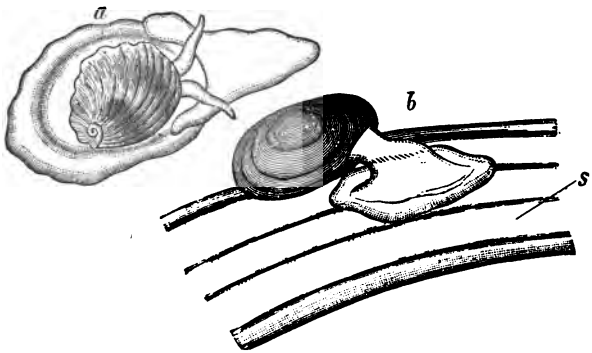

FIG. 60.—Creeping Mollusca. *a*, *Natica*, which can extend its foot very widely; *b*, *Erycina* (?), which creeps by means of its foot, like a univalve, on the skin of a Synapta.

they resemble many water plants, qualify them to live even in strongly agitated currents.

Creeping creatures, which attach themselves only temporarily to stones and plants, and can quit them at pleasure, have special organs of attachment. Thus, in most univalves and some bivalves, the part known as the foot serves this purpose; the broad under-surface clings closely to the object they adhere to, but at the same time can leave go of its hold. The force, however, with which the foot adheres is not merely not absolute, but is even relatively different in individuals of the same species at various ages. In the course of my experiments on the pond-snail (*Limnæa stagnalis*) I found that those just come

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from the egg have so little clinging power in the foot, that the feeblest current suffices to sweep them off the leaves on which they seek for food, although the clinging surface is just as large in proportion to the length of the shell as in the fully grown snails, but the older ones can move about freely in a current of moderate strength. Dr. Kobelt, in Frankfort, took occasion, when discussing my experiments on Limnæa, to show that this fact tends to explain the remarkably wide distribution of this mollusc. It usually lives in ponds and lakes; sometimes, however, it is found in brooks or rivers where the current is feeble; but in these, only fully grown specimens are found, and they are by no means so numerous as in stagnant waters. Hence we may infer that they were carried by floods into the stream at these spots, when already half grown, while the young ones transported at the same time perished for lack of food, in consequence of their inability to cling to leaves in the current. Multiplication in a strong current is equally impossible to the Limnæa, and for the same reason; since, even if the young escaped from the egg, they must shortly perish in consequence of the weakness of the foot. This explains why *Limnæa stagnalis* seeks situations where the water is stagnant, for it is only in such spots that the conditions of life are suitable to every stage of its growth. It would be interesting to institute similar experiments with other species of Molluscs, and I have no doubt that the results that might thus be obtained would contribute to explain many facts hitherto inexplicable as to the distribution of fresh-water snails.

In some cases an increase of clinging power is accompanied by peculiar modifications of structure in the creature itself, which may perhaps be even regarded as its direct result. Among the fresh-water Univalves of the tropics of the eastern hemisphere there is a genus, *Navicella*, which is identical with *Neritina* in all the essential characters of its anatomical structure.[99] Both belong to the same family of univalves, and bear a calcareous plate on the hinder part of the foot, known as the operculum (see fig. 61), which is commonly of the same shape as the mouth of the shell, so as to close it perfectly when the animal draws in the foot. But, in order to do this, it must necessarily leave

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its hold of the object to which it is clinging, and, in point of fact, many Neritinæ attached to stones fall off at the slightest touch. There is no doubt that they thus easily escape from the pursuit of their enemies, precisely as many beetles living on leaves elude the search of the entomologist by dropping off them. If such a Neritina were suddenly transferred to a rushing mountain stream, it would undoubtedly soon be crushed by the rolling of the pebbles, if it preserved its habit of falling at an unexpected jar.

All animals possessing this peculiarity are, therefore, unfitted to live in currents of any force; and the creeping creatures living in such a situation must be able either to hide in the narrowest cracks and fissures in the rocks, or to bore into the earth or the stone itself, or else must have such clinging powers of the foot as may enable them to resist the shock and pressure of the water by attaching themselves firmly to the rock, and applying the margin of the shell so closely to the surface of the stone that it is difficult or impossible to remove them. This is in fact the case; all the Neritinas that I found clinging to the surface of the rock in exposed spots in the mountain streams of the Philippines, adhered as closely as possible, as soon as I touched them. But in this respect many Navicellæ are still better qualified; they often live in the midst of a dashing torrent, adhering to the stones by suction, so closely that it is difficult to raise them, even with a knife, without injuring the margin of the shell. This is effected partly by the sucking power of the foot and partly by the form of the shell, which is flattish, conical, and oval, and has an operculum which is smaller than the marginal circumference of the shell. The relatively small size of the mouth is owing to a calcareous plate forming a sort of half-deck across the back of the inside of the shell, and which may be considered as identical with the inner whorl of other Univalve Shells, while the foot is so broad that it quite covers the under surface of this half-deck, while its margin corresponds exactly with the oval of the mantle, and also corresponds with that of the shell. If a Navicella is removed from the spot to which it is clinging—and this is not difficult to do if it is taken by surprise—it can be seen at once that the animal cannot

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bend up its large foot and withdraw it completely into the shell like other univalves; even when it is plunged at once alive into spirit, the foot remains rigid and almost straight. Thus an operculum placed on the hinder surface of the foot, as in Neritina, would be useless, since it cannot serve to close the opening and to protect the soft parts, if the foot cannot be withdrawn; but the Navicella, as has been said, does not need any such protection, since it clings more closely to the rock when threatened with danger, and we might expect to

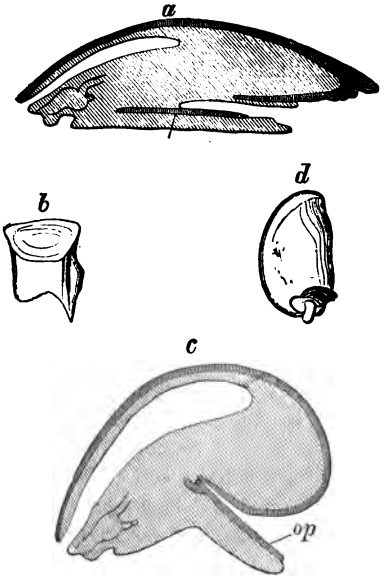

FIG. 61.—Diagram of section through *Neritina* and *Navicella* to show the position of the operculum in each genus. *a*, *Navicella* (*op*, operculum), *b*, operculum of *Navicella*; *c*, *Neritina* (*op*, operculum), *d*, operculum of *Neritina*.

find, on examination, that it had no operculum. In this, however, we should be quite mistaken; in all the Navicellæ, without exception, there is a true operculum placed, exactly as in all the Operculata, on the back or upper side of the foot. It agrees too in structure with that of Neritina, but it is much smaller than the mouth of the shell (fig. 61), and the little hook which serves to attach it to the muscle of the foot, and

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which in Neritina is very small, is modified in Navicella into a large thin plate appearing as a direct prolongation of the free portion of the operculum; finally this lies in a small fold between the back of the foot and the horizontal deck inside the back of the shell. Thus it is evident that the operculum of Navicella comes under the head of rudimentary organs, for it can neither revolve through an arc of 180°, as it would have to do to close the shell, nor could it close the aperture even if it were brought into the proper position. Now, as Navicella is in every other respect a true Neritina, it may be regarded as one which, by long inurement to living in rushing mountain streams, has had its shell modified in the way most suited to those conditions, while the operculum, in consequence of long disuse, has become a peculiar degenerate or rudimentary organ.[100]

The foregoing cases show us that sometimes even the weakest currents may act as potent means of selection between different species or individuals, and they also prove that animals nearly allied, or individuals of the same species, may be qualified at different stages of growth to resist the strongest currents or the most violent shocks by some modification in their mode of life. The characters thus developed clearly exhibit their connection with the creature's mode of life, since its power of resistance evidently depends on them; and in the instances where, as in Navicella, rudimentary organs occur, their derivation from organs formerly of physiological value may be attributed to the indirect action of the currents. But it must not, at the same time, be forgotten that the degeneration of an organ is, in point of fact, no more *explained* by its disuse than the continued existence of a still serviceable organ, as *e.g.* the eye, is *explained* by the fact of its utility or by the evidence of the vast importance of its use.

Nevertheless, there are a few instances in which the direct effects of more or less constant currents of different force on the form of certain animals admit of easy proof.

The direct mechanical effect of currents on the structure and growth of animals.—It is evident that this influence cannot be exerted in any considerable degree on any but fixed animals, at any rate in such a way as to modify or determine

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their growth; and it is plain that if freely creeping or swimming creatures are exposed to it they will probably in most cases be destroyed. Sometimes, however, these are capable of escaping its effects by their own strength.

This occurs, for instance, in the case of many Mollusca, of which the shells are often much injured by erosion. All conchologists are well aware that the shells of fresh-water Mollusca in particular are generally more or less eroded; in many places it is very difficult to find any number of certain species of shells that are not thus worn away, and the process commonly begins at the apex of the shell. It can hardly be doubted that there are very various causes for this; in many cases, which I myself have observed and studied minutely,

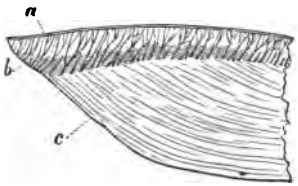

FIG. 62.—Oblique section through the shell of a fresh-water mussel, *Unio*. *a*, Cuticle, external and organic; *b*, the Prismatic Layer next to it; *c*, Nacreous Layer, slightly magnified.

two causes have combined—namely, the boring powers of the filaments of certain Fungi and the constant wear of fresh-water currents, by which, in the Philippines, the shells of various species of *Melania*, *Navicella*, and *Neritina* are attacked. How this occurs can only be understood by briefly studying the structure of such shells.

In the shells of Bivalves as well as in those of Univalves three typical layers of structure may be distinguished: the outer one consists invariably of purely organic matter, known to conchologists as the epidermis; the two inner layers consist of calcic carbonate, combined with a very small quantity of feebly developed organic matter. The outer layer of these two is commonly designated as the prismatic layer; the inner one as the mother-of-pearl or nacreous layer.[101] In most of the Mollusca living in fresh water the external organic layer

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is, relatively speaking, of considerable thickness, very tenacious, and perfectly impermeable by water; and there can be no doubt that, merely by its resistance to the action of water, it serves to protect the calcareous inner portion of the shell against its solvent and destructive effects. Indeed, this is proved by the subjoined sketches of one or two shells, of which the calcareous layers have been deeply eaten into, while the organic cuticle hangs about the shell in thin rags, as it were, above the holes or pits (fig. 63). The question now is: How did erosion first begin in these cases? For, though it would be perfectly intelligible that the face of the calcareous layer, when once laid bare, should be easily eaten into by the action of the

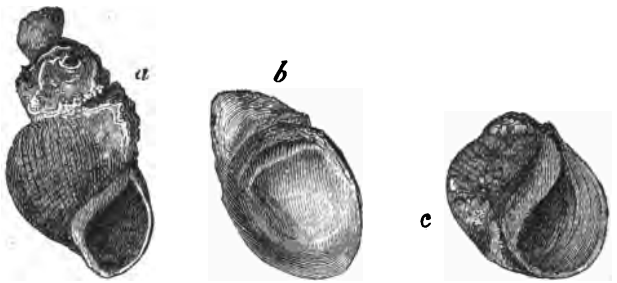

FIG. 63.—Shells of living molluscs partly eroded. *a*, *Melania*; *b*, *Navicella*; *c*, *Neritina*.

carbonic acid in solution in the water, it must have been perfectly protected against this action by the cuticle so long as it remained perfect.

Microscopic examination of the shells here depicted has shown that the substance is penetrated all over, but more especially in the immediate circumference of the eroded spots, by innumerable perforations caused by a minute boring Fungus; these perforations are usually perpendicular to the surface of the shell, and might easily be supposed to be a normal peculiarity of its texture. These boring fungi are also to be found in shells which appear to be perfectly sound, being still completely enclosed in their brown cuticle, while others are already slightly eroded at the apex. This supplies us with the required explanation. The boring fungi, of which the spores are con-

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stantly being carried down towards the shells by the water, attach themselves to the most prominent portion, which is at the same time the oldest and has the thinnest cuticle; they gradually penetrate the shell, and thus the calcareous layers are exposed to the action of the water; this, in consequence of the carbonic acid it contains, eats into the prismatic layer, and, as a minute vortex must be established in each little hole by the action of the current, the chemical effect may be enhanced by the mechanical action of the stream. By degrees this erosion proceeds more rapidly than the destruction of the cuticle by the action of the fungus, and thus long strips or rags remain free, covering the pits worn by the water. The pits at last show to some extent unmistakable traces of the chiselling action of minute whirlpools.

Of course, in time, these will gradually eat through the nacreous as well as the prismatic layer, even without the assistance of the fungus, and finally the soft portion of the animal itself will be laid bare. The creature protects itself against these injurious effects simply by secreting fresh layers of calcareous matter, and thus the structure of the shell is considerably altered. It is certainly difficult to understand how the creature is able to secrete a new supply of calcareous matter precisely at the spot where the shell grows thin; for this does not take place in the first instance only when the shell is actually worn through, but without exception, on the contrary, at a much earlier stage; as is proved by the fact that shells pierced quite through are never, or extremely seldom, found. It may perhaps be assumed that the impact or pressure of the whirlpool is more perceptible at the thinner portions of the shell to the creature within, until at length the local irritation it produces excites a more copious secretion of the shell-forming fluid by the skin. Thus the same power which is exerted to destroy the shell at the same time incites the animal to defend itself against its injurious effects.

Similar results from currents on the animals living exposed to them, whether free and creeping or occasionally sedentary, could be pointed out in many other cases; thus, for instance, the forms of the shells of many univalves seem especially

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adapted to resist pressure or impact in a certain direction. In the total absence of any exact knowledge on this point, we may set such cases aside and address ourselves to the investigation of those where the mechanical influence of a constant current is, by itself, of manifest importance in modifying the growth of fixed or sedentary animals.

In this respect the Coral animals are of predominant importance, for in all the species, large and small, the tendency is conspicuously manifest—and in the individual Polyps as well as in the whole mass—to exert the vigour and direction of their growth to counteract the strength and direction of the current or pressure they may be exposed to. On the other hand, the question as to the way in which the growth of Corals may be affected or modified by external circumstances is of the greatest importance with reference to Darwin's well-known theories as to the origin and formation of coral reefs. We should have no occasion to give much attention to the phenomena I allude to if they either simply availed to confirm Darwin's views, or, on the other hand, in no way affected them; but as they elucidate in detail the same views, antagonistic to Darwin's, which I have gradually arrived at after a careful investigation of the whole mode of growth of coral reefs in general, I feel called upon here to describe them fully. The high authority which every opinion expressed by Darwin has, and always must have, in my estimation, would of itself justify our giving our best attention to a thorough investigation of any question bearing upon them; and it seems all the more permissible in this instance, because the easy application of Darwin's theories of coral-reef formation, their extreme simplicity, and partly also the great interest which has always been excited in the popular mind by the processes of coral growth, have made them almost universally known to the geologist as a convenient hypothesis, and to the layman as one easily grasped and understood. In the following disquisition I shall proceed from special cases, and afterwards discuss the more general question.

A. The influence on growing corals of a constant current produced by other animals.—So long ago as the year 1837 Stimpson described a small crab, under the name of *Hapalo-*

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carcinus marsupialis, which had been discovered in the Pacific Ocean by Dana, in the course of his great voyage under the command of Wilkes. Irrespective of other peculiarities, this was distinguished from all other crabs by a remarkable pouch in which the female carries the young, formed by a prolongation of the lateral plates of the abdomen. Subsequently Heller described another species of crab from the Red Sea, under the name of *Cryptochirus coralliodytes*, of which the female has egg-pouches similar to those of the other genus, but the form of the body is otherwise quite different. While the general form of *Hapalocarcinus* is lenticular, *Cryptochirus* has a thorax of perfectly cylindrical shape, with a head terminating obliquely, so that it strikingly resembles several of the cylindrical wood-boring beetles. The singular mode of life of these crabs was, however, unknown to both these naturalists.

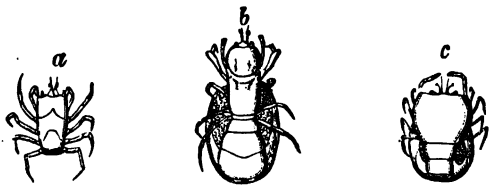

FIG. 64.—The crabs forming galls on corals. *a*, *Cryptochirus* (male); *b*, *Coralliodytes* (female); *c*, *Hapalocarcinus marsupialis* (female).

As I was able to study both species alive in the Philippine Islands, I will here give my observations in detail.

For both of them an association with living Corals is indispensable, and the influence of the Corals on the Crabs is as direct and important as that of the Crabs on the Corals. *Hapalocarcinus* [102] has hitherto been detected only in pieces of branching coral; I have found it on *Sideropora digitata* and *palmata*, and on species of *Seriatopora*; Verrill found it on *Pocillopora cæspitosa* in the Sandwich Islands, and D. Graeffe discovered it on two species of *Seriatopora*. On all these corals the crabs produce a peculiar excrescence on the twigs (so to speak) of a branch; these growths, which are sometimes very broad and massive, and sometimes very slender, grow opposite each other in such a way that the crab settled between them is perfectly

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surrounded, and thus enclosed, in the gall which gradually forms.

It is not difficult to infer what the whole process must be from the different stages observable on one single mass of coral. A diseased excrescence is first produced by the young crab establishing itself between two branches, and the twig thus originating takes various forms according to the character of the species of coral. This is very conspicuous in the different specimens lying before me. In the Seriatopora, both the twigs are leaf-shaped and beset with more or less numerous offshoots terminating in sharp spines; in the more solid Pocillopora the

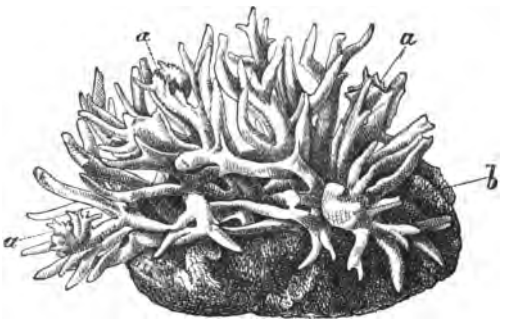

FIG. 65.—*Sideropora hystrix*, with galls inhabited by *Hapalocarcinus marsupialis*. *a a a*, young galls still half open; *b*, an older one, closed, in which a close inspection may detect two opposite fissures.

twigs also have spines, but they are more massive; finally, in Sideropora, spines are wholly absent, and the two twigs between which the crab lives are altogether more massive. In the first instance the two leaf-like twigs are of course far apart, so that the crab could easily get in and out; but as it does not do this it is soon so surrounded by the growing together of the twigs, that it must remain a prisoner. The creature requires a constant and rapid renewal of the water in the gall in which it lives, for the purpose of respiration; at first the water finds a free passage on all sides, but when the two twigs have bent over towards each other, the space through which it can find entrance and exit must grow narrower and narrower. Moreover, from the structure exhibited by galls broken off from

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the coral, it may be concluded with certainty that the crab moves about very little in the cavity, for otherwise we should not find the very distinct scars which are evidently produced by continual scratching in one spot. Since, in all the crabs of this group, the current of water for breathing enters the body close to the mouth, and passes out again at the hinder margin of the branchial cavity, the stream passing through the gall must always flow in one and the same direction. The results are easily recognisable in the half or wholly closed gall. The two excrescences on the coral grow together quickest in those spots which are least exposed to the current through the gall; there also they first come into contact, till at length only two fissures, more or less wide, are left, which plainly show, by their position opposite to each other, that it is through them that the current for respiration passes; one fissure serves for the influx, the other for the exit, of the water. These two slits remain open so long as the crab is alive; no living crab is ever found in a closed gall, and they are for the most part perfectly empty.

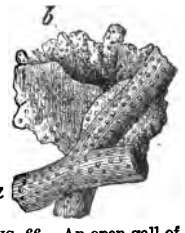

FIG. 66.—An open gall of *Seriatopora hystrix*. *a*, the normal development of the coral: *b*, the gall with a cavity—here laid open—in which a crab was enclosed.

It is impossible not to conclude from this state of things that the fissures are kept open by the force of the current flowing through them; but still this can only occur when the force of the current is exactly commensurate with the strength working in antagonism to it, which is exerted by the growing polyps. These are constantly tending, as is shown by the different stages of the gall, to reduce the space between the two sides of it; at first this may be quite easy, but as the force of the current is gradually increased by the diminution of the fissure, at last a state of equilibrium must be reached in which the forces neutralise each other. Thus, though in the first instance the coral was able to continue its growth unhindered, after the manner of its species, it ere long found an obstacle, which it was unable to contend with, in the current produced by the crab. Hence we are justified in supposing that similar

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hindrances, which might be opposed to the growth, in any spot, of much larger masses of coral, would check or modify their growth in the same way.

I may for the present postpone the application of the principle thus arrived at; but it will repay our trouble if we direct our attention to some other phenomena observable in these same galls. The walls of the leaf-shaped excrescences that

FIG. 67.—*Sideropora palmata*, with a gall which is hardly visible from outside, but shows a distinct fissure dividing the two halves of the closed gall.

form them bear polyps not only on the outer surface, but on the inner surface as well; this is proved by the fact that both are closely covered by little depressions, which, from their structure, can only have been formed by polyps. Now, as the polyps situated in the cavity were just as much exposed to the effects of the current as those on the margin of the fissure, they must show the traces of this influence, if indeed any such influence has been exercised during the growth of the gall. This is, in fact,

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quite unmistakably the case. Not one of the cups is normal in structure; the depression, which in the external polyps is very deep, is here no more than a shallow pit, and the *septa* (or party walls) of the cup are very slightly developed. Hence it follows, with some degree of certainty, that the polyps on the inner surface were not able wholly to overcome the resistance of the current passing over them. This direct action of the stream is unmistakable in many of the cups, where the polyps were exposed to the greatest force of the current produced by the crab; for they are placed obliquely on the fissure and directed outwards, as they must have grown, supposing them unable to grow against the stream.

We see from this that the current caused by the crab is sufficient not merely to force the diseased excrescence on the coral to take a particular direction, but also to check the growth of the individual polyps quite as considerably, and to divert them from their normal growth.

The influence of the respiratory current of crabs of the genus *Cryptochirus*, which live only in the more massive forms of coral, appears to be exerted in quite a different way. I found them in the Philippine Archipelago in cavities in *Goniastræa Bournoni*, in an undetermined true *Astræa*, which was unfortunately lost, also in an undescribed *Trachyphyllia*; finally I received a new form through A. Agassiz from the West Indian seas, which may perhaps form a distinct genus, though it is very nearly allied to the first. It also lives in a Trachyphyllia.[103] The reader will see that they all belong to the massive corals, and, in correspondence with this circumstance, the cavities in which these crabs live are totally unlike those in which *Hapalocarcinus* is found. Here there are no galls, but merely cylindrical or funnel-shaped hollows, which are never closed during the lifetime of the crab, so that it certainly would be able to quit its position. Nevertheless, it as certainly does not do so; but the species I observed living thrust the forepart of their bodies very far out of their peculiar 'cave-dwellings,' so that only their pouches, *i.e.* the hind part of the body, remained within. The cavity itself exhibits some remarkable peculiarities. The bottom of it, on which the

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pouch rests when the creature has completely withdrawn itself into it, displays the radial septa of a polyp-cup one above another. They there are perfectly distinct, while the side walls of the cylindrical cavity are so completely lined with a thin calcareous crust that nothing can be seen of the perpendicular septa of the polyp-cup. From this it is evident that the young crab, or the larva of it, takes up its abode in the centre of a cup, and so kills the polyp inhabiting it. A specimen now lying before me, with an incomplete cave-dwelling, shows that the crab grows at first at the same rate as the

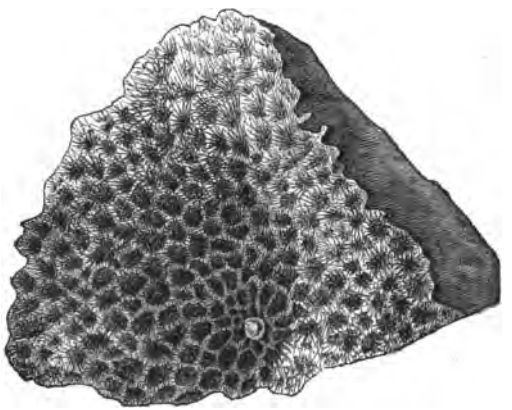

FIG. 68.—*Goniastræa Bournoni*, M. Edw., with a funnel, at the bottom of which a crab (*Cryptochirus coralliodytes*, Hiller) is sitting, only the head being visible.

surrounding polyps; for the margin of the crab's hole, which is perfectly cylindrical, is on exactly the same level as the neighbouring cups, and its breadth too is exactly the same. The cavity is six millimètres long, and the length of the crab found in it exactly corresponds. In another example, however, the length of the pit is twenty millimètres, while that of the crab belonging to it is not more than seven millimètres, at any rate in the dried state. This proves that the crab ceases to grow much sooner than the coral; and this conclusion is strikingly confirmed by the fact that the margin of the cylindrical pit is not on the same level as that of the surrounding polyp-

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cups, but much deeper in. From the margin of the crab's dwelling, properly so called, there is a funnel that widens to the top, and of which the margin, as is shown in the cut (fig. 68), is gradually merged in the upper prominences of the coral. The crab living in the funnel thus formed was carefully observed by me during a long period of its life, and I was enabled to see that it protruded itself far enough out of its hole to be able to reach with its outstretched fore-claws almost to the highest portion of the funnel.

The whole conditions here described [104] allow of no other explanation than the following: At first the crab and the coral grow at an equal rate; for, if the coral grew more rapidly than the crab, an inverted funnel or hollow cone would be formed over the crab, while, if the crab grew the faster, the margin of its cave-dwelling, so long as it was small, could not be exactly on a level with the margin of the contiguous polyp-cups. But when the crab has reached its full length, about seven millimètres, the polyps outgrow its funnel-shaped dwelling, and would no doubt soon wholly overgrow it, if it were not that they find a certain resistance in the current set up by the crab for breathing and in the movements of the creature; and this resistance is sufficient to compel the growth of the coral in a particular and determined direction. The two powers in opposition thus reach an equilibrium, and it is their reciprocal action which gives the funnel its characteristic form.

Here too, as in the former instance, the individual polyps plainly show the effects of the current. While in general the cups are perpendicular to the surface of the coral, in most of those which grow within the funnel this is not the case; they have an oblique direction upwards, and are most oblique where the strength of the current is greatest, *i.e.* at the narrow bottom part of the funnel.

We see thus, in these two examples, that the same force—namely, the respiratory current caused by a crab—affects the individual polyps in the same way, forcing them to grow obliquely; but at the same time it also produces very different effects, resulting from the different law of growth of the two forms of coral-stock. Thus galls are produced only on branched

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species; on the more massive ones, either funnel-shaped or cylindrical pits are formed. In the course of my travels I have made numerous other observations as to the similar effects of currents on individual coral animals and on whole blocks of coral. It will suffice here to select two particularly instructive cases.

One of these bears upon the growth of certain massive species of coral, among which we may especially consider the species of *Porites*, so common in reefs, and a few of the *Astræidæ*. The smallest, and so the youngest, colonies had, as a rule, a regular convex surface; but only, of course, when they were healthy and not eaten away by other animals or by plants. In them the polyps situated at the summit were as well developed as those at the margin of the mass, and they were never left dry even by the lowest ebb-tide. Larger blocks of the same species, which seemed to be more often exposed to the effects of the air, were flat; the polyps at the summit looked feeble, and many of them were dead; indeed, small stones and sand were often lying on the centre of the surface. In still larger masses, of which the upper surface was commonly laid bare by even ordinary ebb-tides, nearly all the polyps at the top were dead, and often entirely covered with sand, *Nullipora*, and other Algæ. The summit of the largest stocks, finally, was concave, with a raised border, from a few lines to an inch higher than the central portion. These old stocks exhibited some important peculiarities. It is well known that even in corals of a massive and solid type there are often slight furrows between the separate cups, and in many stocks of Porites of moderate size these are enlarged to trenches of various breadth. In the largest, again, they have become narrow but often very deep channels which traverse the concave surface and even the raised margin in various directions.

We can, as it seems to me, without any forcing, avail ourselves of the conditions here described to construct a theory of the process of growth of a knoll of Porites. So long as the young colonies are completely under water even at the lowest tides, the separate polyps grow out in every direction, giving the coral an equal convex surface; a section through it gives an outline like that shown in the subjoined wood-

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cut (see fig. 69, *a*). If the growth were to continue equal on all parts of the surface, the polyps at the summit would reach the normal low-water mark sooner than those at the sides; thus, too, they would be the first exposed to the action of the

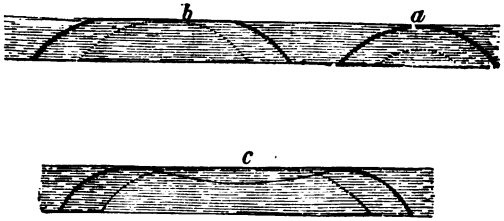

FIG. 69.—Diagram of the growth of the colonies of Porites. *a*, first stage, in which the summit of the coral touches the surface of the sea; *b*, the second, in which it grows only in circumference; *c*, the third, during which the surface, intact at *b*, has died away and been hollowed out.

air and rain at low ebbs, and so die the sooner. The polyps at the sides continue to grow, tending not merely to raise the mass of the coral, but also to extend it horizontally; and thus the upper and rapidly dying surface spreads laterally so much that sand, stones, plants, and various forms of animal life find room upon it. At first this level remains at very much the height to which such a block may normally grow (*b*); but when it has reached a considerable size—from 6 to 8 feet in diameter or even more—the centre plateau is large enough to afford room for the collection of a considerable body of water, with sand, plants, and animals. In consequence of this the upper surface must perish, and then is easily hollowed out by the waves washing over it (*c*). If moreover, in the rainy season, any considerable amount of water falls into this basin at low tides—and that this is possible cannot be disputed—the fresh water collected in it will soon overflow the margin for lack of room. Now the whole coral is very porous, and is always traversed already, as we have seen, by more or less deep furrows. The water naturally seeks these ready-formed channels and widens them, working through the margin in favourable spots where the formation is softest, and thus slowly but surely eating channels through the raised ring round the coral-block. In the cut a diagram of these processes of growth is given.

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Any other explanation appears to me impossible. We might be tempted to account for the elevation of the marginal ring above the central plateau by assuming that it had grown more rapidly than the centre; but if this were the true explanation the wall would be visible even in knolls of moderate size, and this is never the case. Or it might perhaps be said that it is well known that all corals grow most vigorously at the margin of the block, and that the concavity of the upper surface may be easily explained by assuming a subsidence; but the first statement would be simply untrue, and the second perfectly absurd, for at any rate it is impossible to see why such a subsidence should have taken place in the case of the largest masses and not in the medium-sized or small ones. In point of fact, I see no other explanation which agrees so perfectly with the observed facts as that which I have given.

As the last point under this head, we must now consider the way in which the whole reef is affected where it is acted on by currents of different force and flowing in varying directions. I will illustrate this by a highly significant instance which I myself carefully observed.

To the south-west of Mindanao, and exactly opposite the famous old Spanish colony of Zamboanga, is the little island of Basilan. I visited it in 1859, when by far the larger part of it was still occupied by hostile Mohammedans; the Spaniards were restricted to a village at the northern end of the island, which lay opposite to the still smaller island called Malaunavi, separated from Basilan by a narrow channel. This little strait, which, though very narrow, is of some length, runs from north-east to south-west; to the east it opens with a wide mouth into the straits of Zamboanga, while to the west it is barred by a very small island lying between the two others. To this form of the channel and to the particular divergence of the main current in the straits between Basilan and Zamboanga we must ascribe the fact that the current between these islands flows always in one direction, and never changes with the turn of the tides; at least this was the case during the two months I spent there, and it is so throughout the year according to the information given me by Don Claudio Montero, the chief of the

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Commission of Hydrography at that time. The effect of the ebb and flow of the tide is only visible in the increased or diminished force of the current flowing through the channel. Now I willingly admit that possibly a return flow of the current may sometimes take place; but this certainly is not of frequent occurrence, and there can be no doubt that a strong stream passes through the channel for long periods in the same direction. And it is this fact which, above all others, enables us to understand the peculiar structure of the reefs which fringe the islands, and consequently the channel, on both sides. Reefs proper, with a raised margin, do not exist here; the water in the channel is always still, and, as even the waves raised by storms on the main do not affect it, it offers to such small craft as can navigate it a secure shelter in spite of its small extent. But the current is often very strong, running sometimes at from 4 to 5 or even 6 knots an hour.

Both banks of the channel are formed of coral, those of the shore of Malaunavi on the north side being the most developed; they consist of the usual reef-forming species, *Astræa*, *Porites*, *Madrepores*, &c. Now these, like all the species that form large blocks, have a tendency to extend in all directions; but here they are interfered with by the strong current impinging on them at an angle, and flowing, as has been said, during the greater part of the year in the same direction. If it were weaker than the growing power of the coral, its resistance would be easily overcome; but it is, on the contrary, strong enough to force it to grow perfectly perpendicularly. Thus the reef on the Malaunavi side is not more than a few paces wide, with an abrupt perpendicular fall, though the depth is certainly inconsiderable.

The reef which fringes the little island lying in the western outlet of the channel is quite different in its structure. The same species are present as in the channel, but they here grow quite differently in different spots. Where the current is met by the island, of course it parts; thus, at the eastern end of the island, which is that turned inwards towards the channel, a triangular space is found, where the water is full of feeble currents flowing in various directions. Both branches of the

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divided current first strike the island further in, and still at an angle. In this comparatively calm triangle of water, the Madrepores, Astræa, Porites, and other corals do not grow vertically upwards, but on the contrary in all directions, and usually in isolated blocks; and though the branched species generally grow more in height than the more massive forms, even in them it is impossible to overlook a tendency to increase as much in breadth as in height. Hence, on the eastern point of the island there is no perpendicular termination to the reef; it sinks quite gradually to the bottom of the channel. But where the two currents produced by the division of the main stream impinge upon the island, we at once find the perpendicular cliffs again, and the upper surface of the reef is as narrow as in the channel on the shore of Malaunavi. At the opposite end of the island—the western end, that is to say—there is a second calm triangle formed by the meeting of the two streams, and there the reef again assumes the structure which has been minutely described in speaking of the eastern end. Everywhere in the Philippines, and likewise in the Pelew Islands in the Pacific, I have observed the same phenomena; wherever there was an eddy or a calm spot formed between the current and an island, the corals grew in irregular masses, and, more or less, in all directions; and wherever the stream ran parallel with the shore there was an abrupt and perpendicular fall of the reef.

It is not difficult to find an explanation of these phenomena. It is the same as was given above in the case of individual coral knolls; where the sea impinges on coral reefs, with feeble, irregular, and variable currents, flowing in various directions, the reefs, like separate blocks, will be enabled to extend in every direction, since they will not in the course of their growth have to overcome a constant resistance in one direction. But wherever strong and unopposed currents flow constantly in the same direction parallel to the coast, impinging on the reef, the corals forming it must be forced, individually and collectively, to grow perpendicularly—assuming, of course, that their power of growth is insufficient to overcome the resistance of the stream. Between the perpendicular growth thus induced and the perfectly

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horizontal mode of growth not checked in any way, we find every grade of transition. The precipitous fall is more or less oblique as the stream impinging on the reef is more or less strong.[105]

It is my conviction, derived from my own long-continued study of coral reefs, that the connection here indicated between the strength and direction of the stream on the one hand and the vigour of growth in the corals and in the reefs they form on the other, is one of the principal causes that have given the reefs their frequently very remarkable forms. This view is in direct contradiction to Darwin's theory, which now finds universal acceptance, as to the formation of coral reefs. The reception which that has met with, as well as the high respect and veneration which I am most ready to pay to every opinion uttered by Darwin, compels me to devote the ensuing chapter to a detailed description of the reefs of the Pelew Islands in the Pacific, which during ten months I thoroughly investigated. Every variety of reef occurs there within a limited space, and a close study of their structure will show that Darwin's theory is not sufficient to explain them all, but, on the contrary, that in every instance hitherto investigated, whether on a large or small scale, the same effects on their growth, as produced by strong and constant currents, may be detected.

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CHAPTER VIII.

THE INFLUENCE OF WATER IN MOTION—(*continued*).

The Formation of the Coral Reefs of the Pelew or Palaos Islands in the Pacific Ocean.

It is always an unsatisfactory task, and often an unpleasant one, to feel forced to contravene a view which is universally accepted as a true one, and which is supposed to be evidently sufficient to explain all the observed phenomena as completely as is on the whole possible. Nevertheless I cannot here escape this necessity; for it is precisely because I delight to pay to such men as Darwin and Dana the high respect that is due to them, that I find it impossible to be silent on those points where I dissent from their views. The constantly repeated statement that Darwin's theory of coral reefs amply suffices to explain to geologists the origin of fossil reefs would, it is true, scarcely provoke me to a discussion; but I feel that I owe it to Darwin himself, here to state once more the views I hold, founded as they are on a long series of observations. For it seems to me that in the second edition of his universally known work on coral reefs * he has fallen into error as to some observations of mine, inasmuch as he has attributed to me some opinions which at that time certainly I had only very lately held. But it is also due to myself that I should give a more detailed account of them in this place, because Dana, in the second edition of his book on corals which has lately appeared, has not even alluded to my views and observations, although

* *On the Structure and Distribution of Coral Reefs.* Smith, Elder, & Co.

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Darwin himself recognises the force of my objections; though he certainly attempts to set them aside by means of an assumption of which the fallacy is amply proved by the very observations I have published.

The latest labours of the American naturalist prove that his views with regard to the origin of reefs differ very considerably from Darwin's, and in a very essential point. Darwin, as is well known, assumes that wherever fringing reefs occur, a period of elevation or of repose now prevails, while atolls and barrier-reefs can be formed only in regions of recent subsidence. As an essential argument for the correctness of this view he adduces the fact, prominently brought out in a map of his constructing, that active volcanoes occur only in those regions which, from the structure of their reefs, must also be regions of elevation.

Dana agrees with Darwin in so far that he also assumes that atolls or barrier-reefs can only be formed in regions of subsidence; but fringing reefs, according to him, indicate not merely no upheaval in recent times, but, on the contrary, a more considerable subsidence than is pointed to by other reef formations. For instance, he says expressly: 'I still hold that, while barrier-reefs are proofs of subsidence, small or fringing reefs are in themselves no certain evidence of a stationary level, and are often evidence of subsidence, even a greater subsidence than is implied by barrier reefs. I have already stated that one cause limiting the distribution of reefs is bold shores; a wall of rock of even a hundred and fifty feet producing a complete exclusion. . . . Such bold shores are evidence of subsidence; and as only very small reefs, if any, could find footing about such a shore, the narrow reef would be another consequence of the subsidence, and no evidence of a stationary condition.' *

Now, although Darwin admits that, under certain circumstances, narrow (*i.e.* fringing) reefs might be formed on such steep and precipitous shores, he adheres to his former opinion that this does not occur, as a rule, and that, in most cases, reefs of this class prove upheaval in the most recent periods, or even

* *Am. Journ. Sci.* Ser. III. vol. viii. p. 316.

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a process of elevation still going on. He does so, indeed, with the full understanding that his theories would be undermined if he were to accept Dana's views; for it is clear that no theory of upheaval or subsidence, strictly speaking, could then come under discussion. According to Dana's views we may assume that, in regions of general subsidence, local upheavals may occur; and, *vice versâ*, that local subsidence may occur in regions of general upheaval. From this, however, it follows that the structure of the reef itself can give no certain evidence whatever, as the basis of an assertion that this or that region is at a given moment undergoing upheaval or subsidence. Thus to settle this question we must avail ourselves of other arguments than those used by Darwin to establish his theory; Dana in fact seeks for such, and his investigations led him to the conclusion that the whole of the Pacific Ocean is a region of subsidence, while Darwin recognises in it certain distinct regions of subsidence and others of upheaval. Dana further assumes that the West Indian Ocean is at present sinking, while Darwin, on the contrary, regards it as rising, since the reefs occurring in it belong almost exclusively to the group which, according to his theory, ought to prove a condition of upheaval.

Now it might perhaps be objected that, with regard to the formation of atolls and barrier-reefs, both writers perfectly agree, and that the possibility granted by Darwin of the occurrence of fringing reefs on steep and subsiding coasts certainly affords no argument against the view that atolls and barrier-reefs can under any circumstances be formed only during subsidence. This must of course be admitted; but I must nevertheless maintain my opinion that Dana's and Darwin's theories do contradict each other, and that if, as Dana says, all kinds of reefs may originate during subsidence, the structure of the reef itself is of no importance in investigating the question as to whether in any given spot subsidence or upheaval is taking place or has taken place.

Hence it seems to me allowable to ignore Dana's views when the matter in point—as in this place—is to establish in what way the form of the reef has been determined or altered

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by the combined action of internal and external causes. For those forces on which Dana relies for his argument in no way depend on the particular nature of the corals or of the reefs formed by them. Hence we have to deal exclusively with the original unaltered view of Darwin.

There are two modes which may be adopted in contravening or criticising a generally accepted theory. In the first place, its general fundamental basis may be attacked, or, in the second, its value or worthlessness may be tested in a special instance. I shall here adopt this latter method, and am prompted to do so by several reasons. First of all, in this way only is it possible to set in the clearest light the intimate connection between the main subject of this section and the form assumed by reefs, that is to say the direct influence of a constant current on the growth of the reef. But I do so in the second place, in order to oppose the idea that in this particular instance it is difficult or even impossible to test and criticise a general theory by individual examples. Darwin himself, it is true, says that it would be exceptionally difficult to draw any conclusion as to any particular small group of islands or separate atoll or barrier-reef, even when the depth of the sea outside the reef, and the angle at which the enclosed land slopes, are well known. But ought this difficulty—more imaginary than real—to withhold us from making the attempt? I think not. It is usually assumed, and with justice, that the theory which must always lie at the bottom of an hypothesis appears to be soundest when it can be successfully applied in explaining particular cases of difficulty. But this is granting, on the other hand, that we do not simply set aside such difficulties as facts or observation seem to oppose to the theory, because it has already been proved by cumulative evidence. On the contrary, we should rather require that each new difficulty that arises, if only because it is a difficulty, should be applied to test it. The following attempt to refer the reefs of the Pelew Islands in the Pacific—which I myself have thoroughly studied—to their originating causes will plainly show that certain facts, easily explicable according to my theories, present insurmountable difficulties to Darwin's hypothesis.

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I. The general form and structure of the Palaos Islands and Reefs.—The Palaos Islands—the Pelew Islands of English maps—form a small chain lying almost exactly NNE. and SSW., and of which the greatest length, from the northernmost island, Kriangle,* to the southernmost, Ngaur (or Angaur), is about 80 geographical miles. The nearest islands are Sonsorol, about 120 miles to the south-west, and Yap, belonging to the West Caroline Isles, at a distance of fully 150 miles to the north-east.

The structure of these islands is very peculiar. The most northerly group is formed of five small, low islets lying on the eastern side of a true atoll; the largest of them, Kriangle proper, has given its name to the whole little cluster. At about forty miles to the north-west is the bank or reef of Aruangle, which is uninhabited, but which, from the description of the natives of Kriangle, seems to be a true atoll. Due south of Kriangle is the bank of Kossol, which is open to the south-west, and may be described as a horse-shoe atoll. From this begins an extensive barrier-reef which encloses the largest island of the group, Babelthuap. Its northern end is very narrow, in many places scarcely half a mile wide; then it suddenly widens, so that the island towards the middle is about ten miles † or rather more across; its length is about twenty-five miles. The southern portion of the group is composed of innumerable islets, the greater part of them being included in the same reef that hems in Babelthuap; but this, as it runs south, alters more and more in its structure. The most southerly island, Pelelew, marks the end of the reef, though further south still is the island of Ngaur—the Angaur of the maps—which is divided from the others by a very deep channel, and is now surrounded by no reef at all. It is high land, and the surf beats directly on the foot of its raised coral cliffs, which have ceased to grow and which are as white as chalk. A glance at the subjoined map suffices to show that from north to south there is a gradual

* Written as Kiangle or Kyangle on many maps.

† Geographical miles, 60 to a degree.

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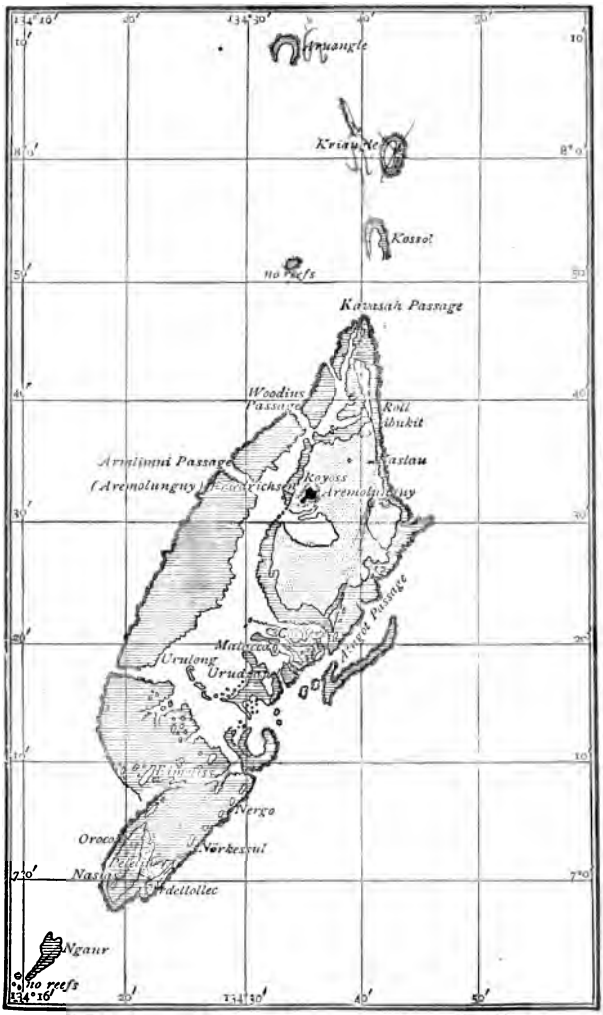

MAP I.—General sketch-map of the Pelew Islands in the Pacific; the deviations from Coello's and Friedrichsen's maps are from my own observations and measurements.

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passage from atolls to barrier-reefs, and then to true fringing reefs, till, at the southernmost end of the group, all reefs have disappeared.

The fact that all the varieties of reef are met with in combination in a district which, in accordance with Darwin's theory, we were accustomed to regard as a district of subsidence, and in which, consequently, only atolls and barrier-reefs ought to occur, is frankly admitted, in the second edition of Darwin's well-known work, to be a very grave difficulty. We might evade this difficulty, as Darwin does—that is, by assuming that even islands which are in process of subsidence, and which therefore ought properly to be enclosed in true barrier-reefs, might sometimes form true fringing reefs, particularly if the fall of the coast were so steep that even during a period of slow subsidence the reef remained close to the shore, and thus preserved the form of a fringing reef. This assumption, however, stands in sharp contradiction to the facts long since observed and announced by myself, and into which I must presently go somewhat more closely. We may also endeavour to overcome this difficulty in another way—for instance, by supposing that within the Pelew Group itself there exists an axis of motion independent of the general change of level of the bottom of the Pacific Ocean. This point might be sought perhaps somewhat to the north of Pelelew, or in that island itself, to the north of which the whole group would be constantly sinking more and more rapidly, while to the south it was rising in proportion. This would, in fact, apparently account for the circumstance that Angaur has hardly any reefs, that Pelelew exhibits fringing reefs, and plainly though feebly developed barrier-reefs. It would also explain why the reefs to the north of this fulcrum become deeper and deeper in the deep sea, till at last, at the extreme north, only atolls occur, or reefs of the atoll character. Now I purposely avoid laying any stress on the fact that such an assumption is in the highest degree improbable, as that there should be such a fulcrum or point of rest localised in so small and isolated a district as these islands constitute in the Pacific Ocean, with upheaval proceeding to the south of it, and subsidence to the north. But, even granting this as pos-

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sible, I believe I have discovered so many proofs of its inaccuracy, notwithstanding its theoretical possibility, in the structural conditions which I have observed in those reefs, that the task of disproving it will not be a hard one. In order to do this thoroughly, it will be necessary to investigate the structure of the islands and of the reefs enclosing them.

II. The atoll of Kriangle.—This is a true atoll of almost oval form, with its lagoon wholly enclosed by the outer reef and the islands upon it; there is no channel leading into it from the sea. In order to get into it, the reef must be crossed at high water at the deepest spot, which is to the south; but even then this lowest spot is so high that it requires some skill to cross it without accident. The lagoon is from three to four fathoms deep, in some places quite five. The bottom, which is perfectly visible through the transparent water, is covered with sand, and on its level surface lie scattered blocks of coral a few feet high; here and there plants are growing on them.

The four islands, only one of which is permanently inhabited, lie on the east side and the south-east end; the most northerly, which, however, does not mark the northernmost point of the group, is alone called Kriangle; the others, counting from north to south, are called Nariungas, Nasingis, and Korack; they are all low, composed of sand, fragments of corals, and large masses of a peculiar stone which consists almost exclusively of the innumerable shells of a recent Foraminifer, the well-known *Tinoporus baculatus*. This creature is now living in extraordinary quantities on the exterior of the reef, and in smaller numbers within the lagoon. The islands are quite flat; the difference in level in their inner and outer edges is not more than a foot or two at most. The rocks of Tinoporus, on the inner side of the islands, lie so high that it is only at high tide that the water touches their base, and they slope slightly inwards towards the lagoon.

The reef which encloses all the islands on the east is but narrow; the outer circumference, as indicated by the breakers at low water, is at most at five or six hundred feet from the shore. It is here quite dead, and exhibits very striking details of structure. It consists of large, almost horizontal banks, covered in spots

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with fragments of shells and corals; these strata are intersected by others lying at from 1 to 1·5 foot lower, which are quite free from detritus, and are formed of blocks of coral so perfectly baked together that in many places they appear to form a homogeneous and compact coralline limestone. Such strata of metamorphosed coralline limestone also occur, but much more rarely, on the summits or inner sides of the islands further to the south. The greater part of this eastern reef is covered by the sea only at high tide; then its surface lies at from 1 to 2 feet below water. Above this the raised margin of the islands stands up from 5 to 6 feet. Its outer slope is steep, and the summit is crowned by blocks of coral of no conspicuous size, which have evidently been carried up during violent storms. The eastern slope of the reef to the sea is not steep, as can be seen by the colour of the water; in the south-west monsoons good anchorage is found here at some distance from the reef.

The reef to the west is devoid of islands, and its structure differs essentially from that of the eastern reef. While this is laid quite dry at every ebb tide, the former cannot be crossed dry-foot excepting at spring-tide ebbs. It follows from this that the western reef must lie from 4 to 5 feet lower than the eastern one; for in so small an island, bathed all round by the same ocean, it is impossible to suppose that this difference can be caused solely by the water being dammed up on the eastern side.

This western reef rises with a not very steep slope from the lagoon; it is moderately broad, almost level, and at first only covered by coralline sand very equally distributed; towards the north and south points of the atoll it rises more than on the west. Nearer to the outer margin of the reef occur living but isolated blocks of coral, at first in small masses and few in number, but the further we go westward the larger and more frequent they become, till at length all sand has disappeared and the blocks of coral are no longer isolated, but a solid, connected mass. Here we rarely meet with dead blocks among the living coral. Of course the coral grows most vigorously outside the external reef. The slope of this western reef, unlike the eastern one, is very abrupt; at a

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distance of from 200 to 300 feet from the outer edge, the colour of the water is as dark as in the channel of Kossol, which is from 50 to 60 fathoms deep. But the most striking peculiarity of the western reef is the accumulation of immense blocks of coral on the south-western point (see Map II.). These are, without exception, dead, and their summits are never covered even at the highest tides, unless perhaps during storms. The largest of these blocks lie on the south-west point, where they not unfrequently measure ten feet or more in diameter; towards the north and east they gradually grow smaller and less numerous, and disappear altogether amid the sand and living coral before the first island is reached on the eastern side; on the western side, going northwards, they extend about halfway. The subjoined map makes this sufficiently clear.

The position of these blocks, and their height above the highest water line, it seems to me can only be regarded as proof of a recent upheaval. It is true indeed, with regard to similarly situated blocks on other reefs, that they have always been said to have been piled up by violent storms; but even Wilkes remarked, as it appears to me with perfect truth, that such enormous stones as are sometimes found on the margin of the outer reefs could not possibly be tossed up so high by waves. For the argument so often used, that in violent tempests even large ships have been carried over the edge of a reef, proves nothing; since a ship will always float if it has enough water under its keel, while a stone always sinks. The blow of a wave may certainly be strong enough to roll such a block a few paces forward on the reef; but even if the force were sufficient to rend blocks of ten feet or more in diameter from the living reef, it certainly would be incapable of raising them over the edge of the reef. In the case now in point the position of the blocks is still more adverse to such an assumption; for on Kriangle they do not lie where the most violent attack of the waves takes place during a storm, but precisely in those spots most sheltered from it. By far the greater number of storms in these islands come from the east; and even though, during the short period of the western monsoon, storms may sometimes sweep up from the west, it is not clear why in this case such

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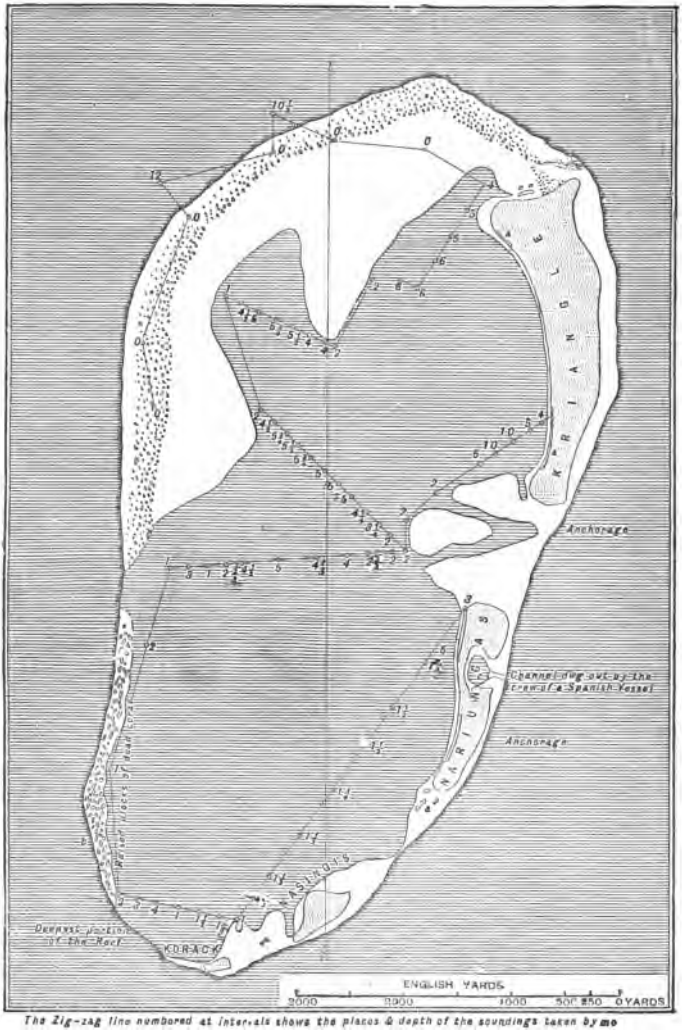

The Zig-zag line numbered at intervals shows the places & depth of the soundings taken by me

MAP II.—The Atoll of Kriangle from my own measurements and soundings.

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blocks should not have been flung up along the whole extent of the western reef. They do, in fact, lie in a spot which may undoubtedly be regarded as the least exposed of the whole reef.

The argument here put forward, and which seems to prove a recent upheaval, can be supplemented by others from which it derives weight. The little island of Nariungas, before spoken of, includes a small lagoon quite divided from the larger one (see Map II.); its mean depth is from 2 to 6 feet, and it is not enclosed by trees on its eastern side, though in every other direction it is hidden by shrubs. This lagoon formerly communicated directly with the sea by a narrow canal which cut through the eastern reef in a perfectly straight line. The natives of Kriangle told me that this channel had been cut by the crew of a Spanish vessel, and a few of the oldest remembered having seen the ship there. The accuracy of this story was confirmed to me by Captain Woodin, of the 'Lady Leigh,' who had called there thirty years ago, and within from five to ten years after that Spanish ship, which had been despatched with others from Manila to these islands for the regular trade in trepang. The channel cut through the reef, and of which the banks are still distinctly recognisable, was too wide for an ordinary boat-canal, and it is probable that it served to admit the ship itself into the small lagoon of Nariungas. The ships which at that time traded with the islands were quite small—schooners of from 50 to 100 tons at most—and such a canal must have been quite large enough for them. But, in its present condition, the reef is raised far too much above ordinary flood-tide to allow of our supposing that the depth of the channel is the same at present as it was then; it must, on the contrary, have been very much deeper if the canal was to be of any practical use. Even now it would be quite superfluous to cut such a channel for boats, since it could be available for them only at the highest tides, when the passage across the reef itself is practicable. The present high position of the canal can thus be accounted for only by supposing that it has been raised together with the reef, and there is further evidence for this in the fact that the lagoon is now much too shallow to admit a schooner; and, above all,

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the canal as it now exists could never have served for it to pass, as in the deepest spots the bottom is only a few feet below high-water mark. Thus everything points to a very recent upheaval, which however can certainly not have been merely local, but must have acted on the whole group of islets which are now known under the name of the largest, Kriangle.

This may be admitted without giving up the opinion that the whole atoll was formed during subsidence; for in order to maintain this view it is merely necessary to assume that the elevation thus proved only began at a very recent period, perhaps at the very time when the Spanish ship cut the channel in the eastern reef. In opposition to this only one obj ction can be raised, but it is one of considerable importance. The great difference above pointed out between the external slope of the eastern and western reefs can hardly be reconciled with the hypothesis of an equable subsidence throughout the atoll; for, if such had occurred, the slope would be equally steep on both sides. In point of fact it is steep only on the west, and on the east very gentle, although this is the windward side. This difficulty, again, might be removed by an arbitrary assumption that the eastern side of the atoll might have remained stationary while only the western side was sinking. This hypothesis also would be easy to upset; but I will postpone the discussion of it to a more favourable opportunity.

III. The bank of Kossol.—The small reef known by this name lies to the south of Kriangle; its shape is a well-defined horseshoe; the channel that divides them is, according to the maps, from 50 to 60 fathoms deep, and, so far as I have been able to detect, entirely free from corals. The channel between Kossol and the northern point of the large island of Babelthuap is, on the contrary, very shallow, at least in comparison with the southern one; on the maps, it is true, a considerable depth is marked, but I must positively contradict the accuracy of these indications; the water in it is everywhere of a pale blue colour, while in the channel between Kossol and Kriangle it is quite dark, almost blue-black. And while in this channel coral-blocks are nowhere to be found standing up from the bottom, they occur in considerable numbers in the channel south of

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Kossol, rising to within from two to five or six fathoms below the surface of the water.

The bank itself is open to the south and south-west, but entirely closed everywhere else. Its outer margin is highest on the east side; on the west there are enormous blocks of coral-line limestone exactly resembling those that lie on the south-west side of Kriangle. At low ebbs the reef is laid quite dry, but its western portion is conspicuously lower than the western reef of Kriangle, since, while I was able to cross the former at five in the afternoon, I had to wait till eight o'clock, even at the lowest portion of the Kriangle reef, before I could get across. The general outline of the reef is oval; it encloses a lagoon, very differently formed from that of Kriangle; for it is almost entirely filled with masses of living corals which vary remarkably in size and form. Towards the south the lagoon gradually deepens, and the blocks of coral increase in size and in number. Towards the other sides the isolated blocks within the lagoon grow together more and more, till at last they form a mass; at the same time, they are so much raised that they help to form, on the reef itself, a spot which is laid dry at every ebb-tide. This inner surface of the reef is not level and sandy, as in Kriangle, but quite rough with knolls of living and dead coral, cut through on all sides by small channels radiating from the centre. We followed up one of these channels, but it only led as far as the outer border of the reef, and we had to wait there a tolerably long time before the tide rose enough to allow us to cross. The outer slope to the west was very abrupt; at a distance of from 150 to 200 feet the water was almost black, and much darker than in the channel between Kossol and Babelthuap. The eastern declivity, on the other hand, was far less steep, as is the case in Kriangle; for the water at some distance from the reef was still quite light blue, and the corals living at the bottom were clearly distinguishable here and there.

Thus, as will have been seen, the structure of the reef of Kossol, and that of the reef of Kriangle, are equally adverse to the theory of their origin by subsidence. With regard to this, one point above all must be brought forward. The reefs are beyond doubt connected, as is proved by the soundings between

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Kriangle and Kossol. Now, if the two channels had been formed by subsidence, as is required by Darwin's theory, it would be quite incomprehensible why, in the channel south of Kossol only, corals should have grown in blocks of various sizes, from the bottom nearly up to the surface, while in the northern channel they are totally absent. For though reef corals certainly do not seem usually to build up from a depth of sixty fathoms, since, on the hypothesis of subsidence, the southern channel must at some time have been high and dry, even the bottom of the north channel must have lain high enough to allow of the establishment of reef-corals. But then it is not clear why they should not have continued to grow up to the present time, and hence, on the theory of subsidence, we might expect to find exactly the opposite of what in fact has happened. But all these difficulties vanish as soon as we suppose that both these channels, and of course the reef also, have been formed during a period of upheaval. In that case the Kriangle channel, which was originally the deeper, would not yet be raised high enough to allow of the establishment on any large scale of reef corals, while the bottom of the channel between Kossol and Babelthuap much sooner attained the requisite level; and it is in accordance with this idea that we find in this channel numerous blocks of various sizes. To this point I must return in a later section.

IV. The northern reef of Babelthuap.—This is a true barrier-reef running round the island of Babelthuap, which rises to a tolerably conspicuous height, and is almost entirely composed of quite recent eruptive rock. The northern portion of the island is extremely narrow, and beyond the northern point lie three or four islets in the channel within the reef. According to the maps hitherto published this would be incorrect: even in the latest by Friedrichsen, founded on data supplied by a naturalist named Kubary, its breadth at the line passing through Aibukit (see Map I.) is made at least three times as great as in mine, constructed on triangular measurements. I found that at this point the width from reef to reef—from east to west—was at most 5 to 6 geographical miles, while Friedrichsen gives it as about 20. The island enclosed by the

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reef is naturally much narrower; starting from Roll, it takes at most twenty minutes to go across the ridge of the island to the east coast. The narrowest part is a little farther to the south; according to my measurements the island here is at most 3,700 feet * wide. In this place, too, Friedrichsen gives the island a breadth of some miles. Close below Aibukit to the south, the island suddenly widens, without, however, anywhere reaching the considerable width of fourteen to fifteen miles attributed to it by Fredrichsen; I am convinced that even at the widest part it is at most from seven to eight miles across.

The reef which runs round the whole of the narrow island exhibits the following remarkable peculiarities of structure. At the northern point and on the west it is at a considerable distance from the land; at the latitude of my house (7° 38′ N.) it was from four to five miles from a small hill on which I had set up my theodolite. Between the inner reefs lying close to the shore and the exterior reef is a channel of from five to six thousand feet in average width, and from thirty to forty-five fathoms deep. This communicates with the ocean by three channels, which certainly do not lie opposite to large rivers or even brooks. The one marked on Friedrichsen's map as 'Kavasak passage' is very narrow, and certainly not navigable for ships. The second, called by Friedrichsen 'Woodin's passage,' is placed by him much too far south; its position is more accurately given on the accompanying map. I passed through this canal with Captain Woodin himself in the 'Lady Leigh' in 1861. The third channel is the widest; it is almost due west from the highest point of Babelthuap, which is designated in Friedrichsen's map as 'Royoss Aremolongui.' The inner lagoon channel runs almost parallel to the coast; it is not very wide, and the depth varies between thirty and forty-five fathoms, and into it debouch, almost all at a right angle, a number of channels which intersect the surface of the shore reef in all directions; one of the last led us as much as 1,200 paces inland at high water, and we there anchored close to the perpendicular bank of living coral which formed the shore of the canal.

* German feet, about 3,810 English feet.

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Here, to the west and north, the reef, so far as it belongs to the island of Babelthuap, may be regarded as a quite characteristically formed barrier reef. According to the prevailing theory—which, however, I am contending against as to its general validity—we ought to infer that a subsidence has lately taken place in this island, since it is in this way only that a barrier reef, as it is said, can originate. I of course cannot admit this proposition as correct, since I dispute the whole argument on which it is founded. But, quite irrespective of this, the eastern reef at the northern end of Babelthuap displays certain peculiarities of structure which directly contradict the theory of subsidence.

For instance, while the western reef stands off from the shore, so that a true channel is formed, navigable for sea-going vessels, this is by no means the case on the north-eastern side of the island. By means of the theodolite, I accurately measured its exact width almost exactly opposite to the village of Aibukit; here the outer reef was distant not more than 1,200 feet in a north-westerly direction—at right angles, that is, to the shore. So far as I could see with the telescope of my instrument, both to north and south, the distance between the shore and reef, as calculated from triangulation, was nowhere much more, and it is not till about the parallel of Athernal that it seems to become greater on the eastern coast, according to Friedrichsen's map. But as the distances and heights of hills are, on the whole, very incorrectly given by Friedrichsen, I see no urgent reason for giving unconditional credence to his map in this particular; however, be that as it may, it is certain, by my own measurements, that in the northern part of the island the outer reef is not more than from four to five hundred paces from the shore. Between them, moreover, there is no reef-channel. The outer reef is no doubt a little raised above the general level of the reef, but not enough to form a channel which ships can navigate; at high tide it is possible to cross it in boats, and in many places it might then be designated as a boat channel. But at low ebbs it is easy to see that no such channel, properly speaking, exists; in many places it would be possible to cross the whole reef on foot, almost dry-

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shod. The surface is, however, traversed by numerous channels running in all directions, without any arrangement, and frequently ending in a deep hole. Nor are there here, as on the western side, true passages; for though the outer reef is cut through in a few places, these channels nowhere lead to a navigable deep water canal. Hence the natives, when going out to sea, never follow these rifts in the reef, but steer across in a straight line for the outer edge of the reef, where they seek a spot low enough to allow them at high tide to float across the raised wall of the reef by skilfully availing themselves of the high surf dashing over it.

The structure of the reef, as we see, is here essentially dissimilar to what we ought to expect on the hypothesis of subsidence. However, this deviation from the normal conditions may be explained in the way actually attempted by Darwin—by the assumption that on the more precipitous east coast the reef necessarily comes nearer to the shore, and that consequently so deep a channel would not be formed as has been the case on the western side. A very successful passage across the eastern reef out into the open sea, however, provides me with an argument against this hypothesis, of which I have already made use in a former small communication on this subject, which has, however, remained unnoticed by both Darwin and Dana. It was on the occasion of my passage to Kriangle. After crossing the reef early in the day, at about nine in the morning, I occupiod myself for several hours till the afternoon on the outer edge of the eastern reef, being favoured by most beautiful weather. My investigations yielded a result which at that time I thought very unsatisfactory; I saw plainly that the reef certainly does not fall abruptly into the sea, as it ought according to theory, but that its slope, on the contrary, is quite gradual. I could push some thousand paces straight away from the reef seawards without losing sight of the bottom; the separate blocks of coral lying there were plainly distinguishable in their various forms. The sea was almost still, but in a great ocean it is never free from that slow swaying motion known as a 'swell.' This exhibited perfectly the phenomena observable on all shelving coasts; *i.e.* the upward wave rises more and more strongly as

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it nears the land, but very equably and hardly perceptibly to the eye, till it breaks at last on the wall of the outer reef with a roar; but as this wall does not rise abruptly from the deep purple sea, as on the western reef, a phenomenon here becomes visible which may frequently be observed on sloping coasts; a second line of breakers succeeds the outer line, nearer in, and often even a third. This phenomenon is very familiar to the natives; to escape the danger of their boats filling at the second or third line of breakers, after crossing the first row of breakers, they shove the boat with long poles as quickly as they can over the outer level of the reef, so as to pass as rapidly as possible the two dangerous lines of surf lying beyond. On the western reef, on the other hand, there is never more than a single broad belt of breakers.

These facts alone suffice to prove that the outward slope of the eastern reef is quite gradual. I investigated the matter very carefully, and with the express view of forming my own judgment on the assertion I had so often read that, on the weather side of a reef, the fall was always very abrupt. But my own investigations were certainly not favourable to this statement; on the contrary I saw, as I have said, that even at some thousand paces from the shore the species of corals were still easily distinguishable, and at a distance even of from two to three sea-miles from the outer reef the water was still much lighter in colour than in the channel between Kriangle and Kossol, where, according to the soundings of navigators, it is about sixty fathoms deep. This exactly agrees with those observations as to Kossol and Kriangle which I mentioned before, without, however, adding much to their significance. But I may now assert with the utmost decisiveness that everywhere in the northern part of this group of islands the eastern slope outside the barrier reef is particularly gentle, while that on the west is so precipitous that, at a few hundred paces outside the reef, the bottom is quite invisible.

The facts here adduced are wholly irreconcilable with Darwin's theory of subsidence. Before entering on that question more in detail it will be well to make an equally exact survey of the reefs lying to the south.

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V. The southern reef of the Pelew Islands.—The most southerly point of Babelthuap is connected with a perfectly irregular system of islands of various sizes, and of the most dissimilar form and structure, which are separated by channels, some very narrow and others of considerable width. They are most numerous close to the main island, and more and more scattered as we proceed farther to the south. Quite to the south the single island of Pelelew is enclosed by the lower end of the great barrier-reef. The character of this reef, which surrounds the elevated islands, alters conspicuously as we pass from north to south, but this change is not gradual. As far as the latitude of Coroere (Corror on Friedrichsen's and some English maps), the channels between the outer reef and the islands become on the whole somewhat shallower, but the difference is not great; nay, in many spots, as, for instance, in the eastern passage into the harbour of Coroere, they attain at least as great a depth (according to Friedrichsen, whose map may in this matter be relied upon) as in the western channel at the latitude of Aibukit, and in this median region of the islands the reef, both in the east and west, lies at a considerable distance from the land it encloses.

Farther to the south, however, the condition of things alters considerably. From about the latitude of Urudzapel (Urucktapel of some maps) the two sides of the reef rapidly close in towards the islands, till Pelelew exhibits a barrier-reef with a shallow boat channel on the north-west side only, while the south and the whole east side are surrounded by a true fringing reef close to the shore.

Even the barrier-reef to the north-west of Pelelew is scarcely to be called a barrier-reef; its outer edge is at about 600 paces from the shore; the surface of the reef, like that of the eastern reef of Babelthuap, is only navigable by boats, and at high water; a true channel is wholly wanting, and the reef is merely intersected by a great number of smaller canals of various widths and depths, as is the case on the eastern reef of the northern island. Finally, its outer margin is not much raised. However, this portion of the reef of Pelelew may certainly be designated as a barrier-reef, though with a certain

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straining of the term; but there can be no doubt whatever that to the southwards it very gradually passes into a fringing reef as characteristic as any to be found in the Philippine Archipelago; and those islands, according to Darwin, may with the greatest certainty be classed among those which, being surrounded by fringing reefs, ought to indicate a region of recent upheaval.

The space included within this southern reef exhibits a few significant peculiarities. No true deep channels occur here, and where they do occur, about the border region near Coroere, they soon disappear as we proceed southwards. The western and eastern reef, enclosing the numerous small islands, surrounds, on the contrary, an almost horizontal level which from west to east may be at least ten nautical miles across; and, extending from the southernmost point of Pelelew almost to Coroere, it is about twenty-two miles long. This enormous and, as has been said, almost flat surface is traversed in every direction by numerous channels intersecting it at right angles. The average depth of this pool itself may be a few fathoms, but on its northern side it suddenly falls to the depth of the channels there, namely, from fifteen to twenty fathoms. On the east side the reef becomes at last so decidedly a fringing reef that natives are always forced to gain the open sea if they wish to visit the villages lying on the east coast. Towards the north again, in the vicinity of Malacca (see Map), this fringing reef becomes a barrier reef. Finally, it must be observed that here, to the south, the eastern and western reefs show the same differences as I have already described minutely in speaking of Kriangle; those to the west generally seem to lie deeper than those on the eastern side, and they are strewn with numerous large blocks of dead coral, which are only very seldom covered by water at the highest flood tides; those on the eastern side lie, on the whole, at a higher level, are formed almost entirely of dead coral, and large blocks of dead coral are never found on their exterior edge.

VI. The prolongation of the Pelews to the north and south.—It cannot, I think, be disputed that the reefs and islands I have been describing belong to each other; but it is very pro-

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bable that the submarine mountain ridge on which the Pelews stand extends much farther to the north and south. The island of Ngaur (Angaur of Friedrichsen's and other maps) lies almost exactly south of Pelelew, and is divided from it by a very deep channel about five miles wide. Still farther south-west of Ngaur a small shoal is marked on the same map, which is certainly formed of corals, and which has not more than ten fathoms of water over it. Unfortunately I was not able to visit the island of Ngaur myself; the natives of Pelelew, among whom I lived for nearly three months, persistently refused to take me there, because, as they declared, it was possible to land at one point only, and even there it was always very dangerous. They asserted that the reef everywhere clung to the shore, so that it was impossible to land excepting in a quite calm sea. I had already formed an idea that true reefs did not occur on the coast of Ngaur when I had passed between that island and Pelelew on the way hither, and this conjecture was confirmed by the statements of Herr Kubary, who, more fortunate than I, was able to visit Ngaur, and by his account (communicated to the Journal of the Godeffroy Museum) this island is in fact devoid of a reef.

The submarine ridge on which, to the north of Babelthuap, Kossol and Kriangle stand, is indicated in older maps as reaching much further to the north. On this there is a series of soundings extending five nautical miles to the west and north of Kossol, and within these limits, indicated by a dotted line, there is, according to Friedrichsen, a small shoal only shown by the words 'heavy breakers' (*starke Brandung*). Thus there is here a reef of about the same height as that of Kossol, but quite divided from it by a channel five miles wide. Directly north-west of Kriangle there lies the well-known reef of Aruangle, at a distance of twelve miles, yet within the line of breakers marked on the maps. Aruangle seems to be a true atoll; it is always said to be one, and, as I believe, correctly. At any rate the description given me by the natives of the island, which was formerly inhabited, entirely agreed with this hypothesis. An attempt I made to induce the people of Kriangle to visit Aruangle failed entirely,

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and my escort from Aibukit was too unfamiliar with the route, which is said to be not without danger, for me to undertake it without any other guide.

I believe that we may unhesitatingly include these last-mentioned reefs and islands with the Pelew group proper, as belonging to the same system of elevations rising from the bottom of the ocean—a system extending about eighty-five miles from north to south, and measuring ten to fifteen miles at its greatest width. I intentionally say a system of *elevations*, for it seems to me quite impossible to suppose that this group of islands and reefs can have been formed by a subsidence, as Darwin's theory requires us to assume. To make this quite clear, we will endeavour to account by the theory of subsidence for the observed phenomena that I have described.

VII. The theory of subsidence as a means of explaining the origin of the Pelew Islands.—If we suppose that the subsidence has been equal everywhere throughout the group, as must be allowed according to Darwin, it is, in the first place, difficult to see why in the north only isolated atolls, in the middle barrier-reefs, and in the south only fringing reefs, have been formed; and why, farther south still at Ngaur, all reef structure should have almost ceased. According to the predominant views it is allowable to regard the depth of the reef channel of Aibukit as a standard of measurement for the subsidence that has taken place. This would thus amount at a maximum to about fifty fathoms. Now if we imagine the islands in the north to have been raised to a height exactly corresponding to the actual amount of the assumed subsidence, the bottom of the channel between Babelthuap and Kossol, as well as that between this atoll and Kriangle, must have been in the highest degree favourable to the establishment of a growth of corals. But this has not been the case; on the contrary, the channel to the north of Kossol is entirely free from them, and that to the south more or less so. If the form of the reef were indeed due to subsidence only, the present fifty-fathom line of soundings must coincide with the outline, at any rate of the main features of the reef now existing; the facts of the case are precisely the contrary. Hence we must in the first

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place conclude that subsidence alone has not here sufficed to produce the forms of the northern reef of this archipelago; since, for instance, it must have caused the isolated blocks of coral in the southern channel of Kossol to form high reefs, just as much and in the same way as has happened in Kriangle or on Kossol itself.

Thus we are obliged, under all the circumstances, to assume the co-operation of some other force besides subsidence when endeavouring to explain the peculiar formation of the northern reef, but still, without wholly excluding the effects of subsidence. That force, as I believe, can only be sought in the action of the constant currents of the sea; for no other influence which might check the growth of coral—such as sand, ooze in the water, strong streams of fresh water, &c.—can be adduced in explanation of the conditions and behaviour of this reef, nor have they ever come into play in these spots. But the currents which during rising tides here run strongly to the east, and at ebbing tides to the west, might very well have acted on the original furrows between Kriangle, Kossol, and Babelthuap, so as to widen them to channels as these first sank below the surface of the sea, and so have opened the way to the influx of the tidal currents. Thus, *combined with the currents*, subsidence might have produced the form exhibited by the northern reef. However, it has always seemed to me to be a very weak point in the theory of subsidence, that it is evidently insufficient to explain some particular cases, and requires to be supplemented by some auxiliary force standing in no direct causal connection with the theory itself; and I am convinced that many similar instances will be found as investigators begin to take the trouble to study separate reefs more exactly than has hitherto been done.

A second difficulty occurs as follows. I have already stated that the triangle lying between Pelelew, Urudzapel, and the Urulong Channel, constituting nearly a fifth of the superficies of the whole group, is almost level, and lies, in section, at from two to four fathoms under water at high tide. This level bottom consists of solid limestone which, rising gradually, constitutes the numerous islands, composed of the same stone, which are scattered about the surface. It is cut through by

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numbers of narrow canals with perpendicular sides, usually from two to three fathoms deep or even more, and evidently cut into the stone by the action of currents; they grow deeper and broader to the east and north-east, and there ultimately fall into a wide basin, extending as far as the south point of Babelthuap, and between fifteen and twenty-five fathoms deep. The rise of this limestone bottom is just as gradual towards the outer reef—where it appears as its internal declivity—as its slope where it forms the rocky islands; still it nowhere constitutes any portion of the present living reef. These conditions are very difficult to explain by the hypothesis of recent subsidence. If such a process had in fact and exclusively effected the submergence of the limestone plateau, this must have acquired its peculiar structure before this recent subsidence was initiated, which is in itself highly improbable. The whole plateau, on the contrary, with its channels, produces the impression that it has been recently formed during a period of rest or of slow elevation. But the limestone plateau affords even better arguments against the assumption that subsidence was going on during the formation of these reefs. Wherever the limestone islands of the southern region are exposed to the denuding action of the rising tides, a wall like a hollow cornice rises abruptly from the base of the island which slopes up gradually from the submarine level, and its summit, which often overhangs to a dangerous extent, has a growth of shrubs or trees. This hollowed-out base, which would show a highly concave section, is from six to ten feet high; at the highest flood-tides the water rushes into it with great force, and its face exhibits many smaller holes and fissures, often eaten into the solid rock for some feet. In many spots the overhanging summit threatens to fall, and that such catastrophes are certainly not rare, may be seen by the piled-up fragments which in many places lie half in the water at the foot of the islands. This seems to me to prove convincingly that a subsidence has not taken place, for it is not clear how, during subsidence, such a form of the internal limestone plateau and its transition into the islands rising from it could have originated.

It might, however, be conceded that the phenomena here

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described make the theory of a recent subsidence untenable as regards the southern portion of the group, without our being obliged to deny the possibility of such action for the whole group. If, for instance, it is assumed that the subsidence has not taken place equally, but that by a sort of tilt the northern portion has subsided most, the middle but very little, and the south not at all, all the observed phenomena might be accounted for, or at least apparently explained. Nay, more, the presence of true fringing reefs to the extreme south of Pelelew, and the total absence of all visible reefs round Ngaur, would, from the point of view of the Darwinian theory, indicate a past process of elevation of the region south of the axis, if it were assumed that this point of equilibrium and perfect rest had been somewhere near the northern point of Pelelew.

Now I shall lay no great stress on the internal improbability of the hypothesis that such an unequal movement should actually have occurred in so small an area, which, besides, rises from the depths of the ocean perfectly isolated from other groups of islands. Indeed, the difficulties here raised would by no means be removed in this way; they would rather be essentially enhanced, from the fact that south of Ngaur a submarine reef is found very near to that island, and its being divided from it can be explained only by supposing that some other forces have been at work besides subsidence only. Thus even if it were admitted, in spite of the facts which are directly opposed to it, that the impossibility of such a subsidence is not conclusively proved by them, we should still be compelled to acknowledge that the influence of the constant currents must be, in all cases, an essential factor in the history of the origin and formation of these islands. For, to insist once more very positively on this point, during subsidence the coast-line of the sinking island would necessarily be preserved, as Darwin even will admit; but this, as is proved by my data, has not been the case, and hence the subsidence theory, by itself, ceases to be applicable. This, naturally, narrows its whole general value; for if it is impossible in a special case like the present to explain the circumstances by the only force which that theory admits to be efficient and determining, and if, in-

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stead of it, we are compelled to have recourse to various other forces to aid us to a solution, the problem of showing that a subsidence must nevertheless have taken place belongs more than ever to the prevailing theory. But in the case here under discussion such an attempt is met by an insuperable difficulty; this was briefly alluded to above, and must now be discussed somewhat more fully.

The submarine mountain district which serves as the foundation of the whole group is extremely narrow; at the widest part the western reef is at most from twelve to fifteen miles from the eastern one. Nevertheless, these reefs are extraordinarily dissimilar in structure; even in the small and independent atoll of Kriangle this difference is conspicuous. The eastern reef is everywhere much nearer to the shore than the western. A navigable channel between it and the included islands occurs only at about the middle of Babelthuap, where Altngot Passage (see Map I.) has been formed, according to Friedrichsen's map, by an outer reef lying in front of the island reef proper. The eastern reef, so far as I have seen it, nowhere exhibits a line of dead coral-blocks above the highest tide mark. And yet this is the weather side, on which only, it is said, such blocks ever occur. The western reef, on the contrary, is invariably characterised by them. Moreover, while the western cliff is throughout a true barrier reef, almost down to the southern point of Pelelew, the eastern reef can hardly be regarded as a barrier reef even at the north of Babelthuap; and southwards for about the lower third of the group, it assumes the character of a true fringing reef.

This difference, and the incontrovertible fact that fringing reefs predominate on the eastern coast, cannot by any means be reconciled with Darwin's theory unless we suppose, as Darwin has done and as Dana evidently fain would do, that such a reef formation might take place even during subsidence. But, according to Darwin's own admission, this involves the assumption that the seaward declivity of the outer reef is extremely steep. This hypothetical steepness, however, occurs in the Pelew Islands only on the west side, while, in absolute contradiction, the eastern declivity is remarkably gradual. From

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the tops of trees in Kriangle I could clearly discern that there, too, the light hue of the water to the eastward denoted a shelving shore, while on the west the deep blue sea comes close up to the outer edge of the reef. Anchorage can be found outside the reef on the eastern coast, but not on the west, and the same is true of Kossol and the northern portion of Babelthuap. We could venture on the west side close up to the reef in our schooner; in cruising we were not forced to tack till within a few hundred paces of the shore. This would be quite impossible on the eastern side, where for the whole distance from Roll to Kossol I could still clearly see the corals at from one to two geographical miles from the shore. Again, it is now very difficult to enter the harbour of Coroere, formerly a very good one, on account of the numerous shoals and the shelving upwards of the sea bottom, and this I was assured of by Captain Woodin at a time when I still believed implicitly in the absolute correctness of the subsidence theory. Finally, on the western side of Pelelew, where the reef is not a perfectly characterised barrier-reef, the 'Lady Leigh' approached within a hundred paces of the reef, while on the east coast a wide belt of light blue water extends far out to sea.

Here we find a state of things precisely the reverse of what Darwin in the second edition of his book has adduced as an argument against my views. Where, according to him, there should be an extremely abrupt declivity, it is not to be found, and where it does in fact occur, as on the west coast, no fringing reef is formed.

A glance at an ideal but correct section of the Pelews in various spots will here throw light on what I have advanced, and at the same time conclusively show that in this particular instance the principles of the subsidence theory do not suffice to explain the peculiar formation of the reefs. And even if, like Darwin and Dana, we set aside this difficulty, so many, as we have seen, still remain that their theory must call in the aid of other forces—namely, currents—to enable us to understand the structure and origin of these reefs. Hence, inevitably, the question arises whether perhaps the auxiliary cause, which is indispensable to the subsidence theory, may not have

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been the only efficient cause; and, moreover, the further enquiry whether this auxiliary cause, in combination with a slow upheaval, might not have been perfectly competent to give rise to every form of reef, simultaneously and side by side on the same area. Many celestial phenomena can be explained, and long were explained, by assuming that the sun moved round the earth; the consideration that it was insufficient to explain other facts allowed us to perceive its complete absurdity. But it is not always the case that one explanation perfectly excludes the other. We know that in most plants chlorophyll is formed only under the influence of light; an exception is found in many

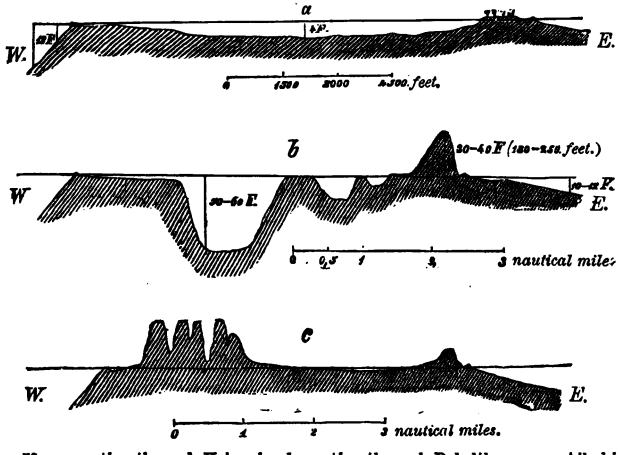

FIG. 70.—*a*, section through Kriangle; *b*, section through Babelthuap near Aibukit; *c*, section through Pelelew.

Coniferæ, in which the same leaf-green is elaborated even in the dark. Hence we must conclude that other causes besides those that act on broad-leaved plants are capable of producing the same results. We know, generally, that nature has in many cases made use of different means to produce results which to our eyes seem identical. Thus, to return to the matter in hand, we still have to investigate the question whether the same results might not have been produced by the auxiliary cause, assuming an upheaval, as by the hypothetical subsidence; since,

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even under the assumption of the subsidence, they still could find only a forced explanation by the help of some other agency.

To guide us in this enquiry, it will be well to collect and collate the facts which may directly prove a recent upheaval in the Pelew Archipelago.

Evidences of recent upheaval in the Pelew Islands.—I have already pointed out that the huge blocks of coral lying on the outer margin of the western reef, in my opinion, can only be regarded as evidence of a recent upheaval. Since, however, this may be disputed on familiar, though not perhaps very strong, grounds, I will not attribute to it any great importance.

The following stronger grounds, on the other hand, can hardly be doubted. Most of the islands are high; to the south they rise to 200 or even 300 feet (at most), while on Babelthuap there are hills said to be 2,000 feet high. Their structure sufficiently proves that they owe their origin to a volcanic upheaval in quite recent times.

Between the islands of the north and south a marked contrast is visible; while the former are almost exclusively volcanic, by far the greater number of the latter are formed of upheaved and partly metamorphic coralline limestone. This contrast is so sharply defined that even the natives have distinctive names to express the difference; the islands formed of coralline limestone they call 'Kokeal,' the volcanic islands 'Royoss.'

A recent work by Dr. Wiechmann treats of the geological structure of the northern islands. This geologist [106] has come to the conclusion, which is confirmed by Herr Gümbel (inspector of mines), who examined my collection of minerals, that the eruptive rock is augitic Andesite. Wiechmann also came to the conclusion—without having been to the islands, and simply from studying the minerals collected there by Dr. Kubary—that the eruption must have been submarine—a view I had long since taken, from a study of the islands themselves. He also approximately determined the period of the eruption; he is of opinion that the upheaval must have taken place during the latest period of the tertiary epoch. A remarkable feature, not mentioned by Wiechmann, is the distribution of the various volcanic rocks in Babelthuap. The solid eruptive rock, Andesite,

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according to my observations, occurs exclusively, or nearly so, on the east side of the island, while, on the west, the lower hills consist of red tufa and strata of rolled pebbles; these are but rarely traversed by the Andesite core which forms isolated high hills. Thus, for instance, the summit of that known as 'Royoss Armlimui' (see Map. I), which I did not ascend, from Kubary's information appears to consist of Andesite, and the black colour of the peak confirms this. These differences in the geology of the country are marked by a corresponding variety in the landscape. While on the western side the slope of the land is generally gentle, and small islets formed of tufa lie scattered on the surface of the inner reef, the eastern side is everywhere much more precipitous. There, where the black Andesite rock rises to any considerable height, we frequently find a quite perpendicular precipice. This is apt to hang over at the top, and its base, hollowed away by the surf, generally slopes to a continuous bottom of the same rock; but we nowhere meet with separate islets, such as are to be seen on the western side. There the strata of tufa are almost horizontal, with a slight dip to the west; according to Friedrichsen's map these also occur in the island of Aruangle, since, from Kubary's account, the natives declare that it consists of 'Royoss.' Certainly the description I had of it in Kriangle does not agree with this. However, be this as it may, so much at least is certain, that at a former period the tufa of the west extended much further than it now does, since a few disrupted islets of tufa lie on the surface of the inner reef at one or two nautical miles from the main island.

At the southern end of Babelthuap the eruptive rocks are combined with the limestone rocks called 'Kokeal.' Still there are but a few spots where they lie directly one on the other. I myself, in fact, have never seen them in such juxtaposition; but Wiechmann states, on the strength of Kubary's observations, that solid limestone lies immediately upon the black Andesite at the south-east end of Babelthuap, a spot I have not visited. Similar examples occur, according to this observer, on two small islands lying to the south of Coroere. But, irrespective of these localities, the islands composed of volcanic rock and of coralline

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limestone mutually exclude each other. In the border region, about the middle of the group, they are mingled without order; thus, for instance, the island of Coroere, consisting entirely of tufa, is close to the limestone islands which lie by the southern point of Babelthuap; then again we find a limestone island, and then the wholly volcanic island of Malacca, and between these larger islands there are numerous smaller ones, some of coralline limestone and some of tufa.

Yet farther to the south the Andesite and volcanic tufa wholly disappear, and all the islands south of the latitude of Urulong (see Map I.) consist exclusively of upheaved coralline limestone, partly very highly metamorphosed. These are, without exception, true raised reefs, as is seen from their general form, the equal level of their summits, and the fossils found in their strata; their structure and their connection with the still living reef prove, too, that they are of quite recent origin. It will be well worth the trouble to study the arguments for this last statement somewhat more closely.

The height of the cliffs of the various 'Kokeal' islands differs greatly; the highest are from two hundred and fifty to three hundred feet above the sea, the lowest often scarcely ten feet above the water. Even in the same island, as in Pelelew, this difference occurs. The western cliffs of this island rise to about 250 feet with a perfectly horizontal top; the eastern cliffs at Ardelollec, on the contrary, are at most eighty feet above the sea; their top, too, is almost horizontal. Quite at the south of the island, again, we find cliffs which stand barely five to ten feet above the sand thrown up by the waves. In general the northern islands of the Kokeal are the loftiest; but even there they certainly never reach the height ascribed to them by Friedrichsen of from fifteen hundred to two thousand feet.

The geognostic structure of the Kokeal islands is also very various. Sometimes the cliffs are composed of very dense limestone in which hardly a trace of fossils can be found, or in which the coralline structure has been preserved; in the latter case the rock is sometimes hard, as if infiltrated by a dense almost crystalline limestone; or it may be chalky, as white as snow, and easily friable. The cliffs of Ngaur and Pelelew,

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for instance, consist of such a snow-white rock, and their gleaming perpendicular walls form a landmark from afar for the sailor. The masses of fossils found in them, both corals and shells, are for the most part merely impressions preserved in the limestone. This is difficult to detect at the first glance; for the corals especially, or rather their impressions, lie so wonderfully closely that they seem to form a dense mass of compressed corals.

The geographical distribution of these different kinds of coralline limestone also offers some striking peculiarities. All the Kokeal islands which I saw, and which lay in the vicinity of volcanic rocks—as, for instance, those in the neighbourhood of Coroere—consist of dense limestone which is often semi-crystalline; when fossils occur, they are firmly imbedded in the rock and preserved uninjured. These islands also yield exclusively the large pebbles of arragonite which are used by the natives of the island of Yap lying a hundred miles to the northward—as a kind of money in great request. The more remote the islands are from the centre of volcanic action presumably situated in the middle of Babelthuap, the less prevalent is the limestone, dense or crystalline, till in the south it finally quite disappears.

The fossils contained in these rocks show, in conjunction with other peculiarities in the structure of the upheaved reefs, that these reefs belong to quite a recent period, and that, in fact, we must regard them only as the beginning of the reefs now in course of construction in the neighbouring seas. On the island of Noerkessul, lying on the eastern reef of Pelelew, which is only about twenty to twenty-five feet high, I found with true Astræidæ, imbedded in the rock, a tooth of the Indian crocodile, which still is found there, though it is not frequent. On the little island of Calacoligoll, which is almost on the outer ridge of the western reef of Pelelew (that is to say not more than 120 feet from it), I found a large block, at least five feet in length, in which the imbedded corals stood upright, and among them were shells of *Pholas* and numerous tubes of *Vermetus gigas*, which still lives and is very common in the sea close by. The centre of Pelelew is from twenty to twenty-

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five feet above high-water mark; the chalk-like cliffs rise from the sea perpendicularly, or at any rate very steeply, and the inner base shows clear traces of the effects of surf at a former period. Here constantly are found heaps of torn-up rocks and fossils; but those fossils which were found on the inner side of the cliffs were quite different from those of the outer side—numerous Fungiæ, which are very near to living species, or may be identical, many Pectens, with enormous masses of two or three species of *Mycedium* and *Agaricia*, belonging to the most delicate forms of the genera. These two corals form the greater part of the rock of which the cliffs consist.

But besides these reasons, already indicated by Wiechmann, for assuming a recent upheaval, there are other factors which confirm this evidence. The eastern reef of Pelelew has all the character of a fringing reef; the outer edge, which is scarcely raised, and which in many places lies at most at 100 feet from the shore, gradually passes into a manifold series of raised cliffs. Those of the first series are mostly only six to ten feet above the strand, which slopes down to the reef; the base is much hollowed out by the waves, and passes without interruption into the surface of the dead reef; it also consists entirely of Astræa and Mæandrina, partly metamorphosed. The surface of the dead reef next to the strand is almost horizontal, but it drops by little shelves hardly more than a foot high, till the lowest of the terraces thus formed is covered at high tide by from two to three feet of water; then, gently shelving down, the dead portion of the reef merges in the living, of which, as I have said, the outer edge is but little raised. All these terraces are quite smooth, and without any trace of large coral blocks thrown up by the waves. From these indications we may safely infer that elevation has taken place within a very recent period; for otherwise it is difficult to see how the still living reef could be a direct continuation of the raised dead coral. Quite identical phenomena are displayed, as I have said, on the east side of Kriangle.

The facts here adduced suffice, as it seems to me, to prove that, in the first place, a quite recent upheaval must have occurred; and, secondly, that that period of upheaval must have

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passed into the present condition of very slow elevation or absolute rest without any conspicuous break.

An attempt to explain the structure of the reefs of the Pelew Islands.—I have said that the theory of subsidence is insufficient to explain the sections given on p. 258, since, according to that theory, on the steep west coast there ought to be a fringing reef, and on the shelving east coast a barrier reef. Exactly the contrary is the case. The occurrence of shallows without reefs close to atolls, as at Kossol, and of high reefless islands, as Ngaur, the high blocks on the west side and outer edge of all the western reefs, the extensive, almost horizontal, submarine level to the north of Pelelew, the uninterrupted connection of the eastern reefs of Pelelew and Kriangle with the dead raised coralline cliffs—all these facts are arguments, hardly to be refuted, against a recent subsidence. And if all of these should be explained away by arbitrary assumptions of which the baselessness could only be proved by fresh investigations carried out on the spot, we still should be obliged to accept the degrading action of the movement of the sea, and, above all, that of constant currents, as causes co-operating with the supposed subsidence. I, of course, readily admit that these must have had their effect, but I positively dispute that the recognition of these effects proves the necessity of a subsidence. On the contrary, I believe that those apparently secondary causes would be far more likely to be effective during a period of elevation than when combined with subsidence, and that all the conditions I have described which argue against a subsidence under the other hypothesis may be perfectly explained by easy and independent assumptions. This, in the first instance, applies of course only to the structure of the Pelew reef, and it must remain for further investigations to determine how far similar conditions may exist or not in other coral islands; since the proof that here, in the Pelew Islands, subsidence cannot have been the special cause which has determined the form of the reefs is, self-evidently, no proof that in other groups subsidence may not have been combined with the upward growth of the reef in the form impressed on it by other causes.

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In the seventh chapter we have already seen that not individual corals only but whole reefs are influenced in the most decided manner by two forces, *i.e.* the strength and the direction of constant currents impinging on them. Their favourable development depends, no doubt, on other things, as the warmth of the water, its chemical composition, the accidental mingling of species, &c.; but all these influences, in my opinion, sink into the background in comparison with currents; for though they may impede or even destroy the existence of the polyps, they never, so far as I can see, force them to develope in any particular direction. Now this, as I have amply explained in Chapter VII., is in an eminent degree the effect of constant currents. Moreover in this investigation it is not our business to determine whether corals can thrive, or even grow at all, in this or that particular spot, but exclusively to decide whether the forms of particular reefs, under circumstances of unhindered growth, can be explained by known causes.

We must remember that wherever constant and deep currents impinge on a coast at an angle, the reef will inevitably grow upwards perpendicularly if the force of the current is sufficient; and, on the other hand, that many species of coral have a tendency to grow equally in every direction, as far as circumstances allow, so long as shallow currents flow horizontally over them.

The high seas, the open ocean, exhibit both these modes of motion of water in the most conspicuous degree. Late researches have shown us that strong currents often flow at great depths; these constant currents maintain the same direction the whole year through, though their force may vary; even those arising from the ebb and flow of the tide vary in strength under the influence of the prevailing winds, but never, or rarely, in direction. Besides these currents flowing at great depths there are, in the second place, quite superficial ones, which are sometimes variable, particularly if they are affected by the prevalent winds, or sometimes very constant, as in the case of the drift in great seas.

The Pelew Islands lie, as is well known, within the region of the north equatorial current flowing from east to west in the

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Pacific Ocean. This current, in conjunction with those caused by the ebb and flow of the tide, impinges perpendicularly on the broad side of the group; hence on their eastern side there is a triangle of comparatively still water, since the main current must part before the insuperable barrier; and, within it, only the more superficial currents can produce any effect. These, however, here in the Pelew Islands flow almost constantly from east to west; on the eastern reef a long line of breakers is always visible even during the short period of the south-west monsoon, and even at the highest tides it is always dangerous to cross the reef here. On the western reef, on the contrary, at high tide and in a calm sea, the water over the exterior edge of the reef is so perfectly still that it may be paddled across in a boat without any danger. The currents which run past the islands to the north and south, or between the separate islands, whether as tidal currents or as part of the great north equatorial current, on the west side, turn at an angle to the north or south. In correspondence with these facts we see that in a rough sea a wave falling on the outer reef propagates itself in the direction indicated, while analogous waves on the east break simultaneously on almost the whole length of the shore. In connection with this, indeed, there is another fact which surprised me very much the first time I observed it. It is usually supposed that while the tide is rising, the water that flows in the lagoons or lagoon channels is thrown into them over the outer margin of the reef. This is certainly not the case in the Pelews; almost all the water flows into the natural channels as readily as it flows out of them. This is proved by the fact that during the rising tide the current produced on the surface of the reef does not flow into the channel from the outer reef, as would be expected if that hypothesis were correct, but on the contrary from the channel towards the reef. During my first expedition on the western reef, my life was in some danger from this circumstance, then unknown to me, for I had gone so far from the boat that I had great difficulty in getting back to it again.

Let us now endeavour to explain the observations I have communicated on the assumption that both these classes of currents were active agents during a period of upheaval in

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these islands. I hope thus to succeed in showing that in this particular instance every difficulty vanishes which can be raised by the hypothesis of subsidence.

In Kriangle the boat-canal cut through the eastern reef, and the large coral blocks lying at the south-west point are easily explained by upheaval, as also the structure of the eastern reef. On the western side the current attacks the reef at an angle; hence it must grow upwards perpendicularly. Thus, by degrees, the corals elevated above the level of the living reef must die out; they remain standing, however, and are slowly destroyed by wind and weather, the softer parts first and the harder portions later, and these naturally endure the longest where they are least and most rarely exposed to waves and storms. This in Kriangle is the case precisely in the spot where the highest blocks lie on the outer margin of the reef. On the eastern side, on the contrary, the ocean drift, combined with the constant current to the westward, falls perpendicularly upon the reef; the billows are still further increased on this side by the gentle slope of the sea-bottom, so that a strong, and above all an unremitting, wearing-down process is exercised on the reef. Here, on the weather side, it is said that the largest thrown-up blocks ought to be found; but this is not the case, and it is easily explained. If we suppose that such blocks were actually thrown up for once, they must soon have been destroyed by the incessant action of the waves beating directly on the reef; and the same is the case naturally with all corals which have been lifted above the highest storm tides during a slow elevation of the outer margin of the reef.

One objection only can be raised. The lagoon, that is to say, which is enclosed by the reefs, might with apparent justice be adduced as evidence against an upheaval. And this would in fact prove a great obstacle to my views if it were necessary to assume a very rapid elevation of the whole archipelago. But as the case is precisely the reverse we must assume a very slow upheaval, and it is easy to offer an explanation of the origin of a lagoon, in spite of a slow rising of the bottom. Reflect for a moment on the instance, discussed in the previous chapter, of

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an old colony of Porites. Its surface, in the first instance quite level, will be gradually hollowed out by various co-operating influences, and so at last a raised margin, only cut through by a few channels, will surround a central hollow. A precisely similar result may be produced in a reef undergoing slow upheaval. Suppose, for example, that Kriangle had a tolerably level surface, like the shallows to the south of Ngaur, or like Kossol, before it was raised to the average level of the sea: from the first moment when it was exposed to aerial influences a process of destruction must have begun on the surface of the reef, perfectly analogous to that which takes effect on large isolated coral blocks. Animals and plants first establish themselves on the surface of the reef, which is certainly highly favourable to them; they excavate and penetrate the solid limestone of the coral in every direction while the rain falling on the face of it kills the polyps themselves; the rain and the sea-water flung over the margin of the reef must remain there if they can find no outlet. In the first instance the water on the summit of such a rising reef may often remain standing, but channels must soon be worn through the constantly growing and rising margin, or submarine drainage may easily arise, since boring animals and plants are able gradually to destroy even the hardest limestone. That there are channels of this kind in Kriangle may be inferred from the fact that at low ebb-tides the water in the lagoon stands at no higher a level than it does outside the atoll; but this could not occur if the water thrown over into the lagoon at high tide did not easily find an outlet through the reef itself, for surface channels, which might serve the same purpose, are wholly wanting. The extreme porousness of the soil of Kriangle below the sea-level is also proved by another fact. The inhabitants have sunk deep wells, and a very large tank, about ten feet deep, for bathing purposes; the water in these is usually fresh, as they fill during the rainy season. But when, after persistent drought in the dry season, the level of the water sinks considerably in the basin, the bottom of it is frequently brackish, and that without storms having arisen to cause the sea-water outside to wash over the low island and into the tank or the wells. This shows that

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sea-water can percolate through the walls of the atoll-reef into these reservoirs, and consequently proves that the soil must be pierced by larger or smaller channels. The raised limestone islands of Kokeal are similarly porous. One very small island close to Coroere has quite the structure of a true uplifted atoll. A high wall of metamorphic coralline limestone surrounds a deep lagoon on all sides, and no channel leads from this to the sea at the present day. There is a little ridge, which may formerly have been a channel, to be crossed in order to reach the lagoon. Nevertheless the same fish are found in the lagoon as outside, the water is equally salt, and its level rises and sinks regularly with the tidal flow and ebb. The following circumstance is even more conclusive. On one of my excursions round Pelelew, before going into the harbour of Nasiass from the sea, I saw out at sea a wide current of yellowish water, almost fresh, flowing from the land; its edge was pretty sharply defined against the sea water. It was exactly low water. The natives informed me that this current was always there, though somewhat more feeble at high tide, and strongest during the rainy season. Now in the whole of Pelelew there is not one stream from which this current could proceed. All the surface water percolates at once through the excessively porous soil, and it is only during heavy storms of rain that drainage streams form in the gullies, and these totally disappear again in a few hours. This water then runs away through the soil down to a certain level. But, instead of reappearing at the same level on the seashore, its flow is submarine for a considerable distance from land—a proof that it must have found its way through very deeplying channels.

If we duly consider all these conditions, it becomes clear that there is no serious difficulty in the way of the hypothesis that the lagoon extant in Kriangle should have been the result of the action of currents on the porous soil during a period of slow upheaval.

With regard to the reef of Babelthuap, there are other objections in the way of the subsidence theory; by far the most grave is the gradual seaward slope of the eastern outer reef. But this and all other difficulties vanish with the supposition that the reefs

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were formed during a period of elevation, if we duly realise in our mind the effects that must have ensued from the combined action of upheaval and of more or less constant currents on the form of the growing reef. To the eastward the impact of the current on the island is perpendicular to the face of the coast; it therefore beats upon the slowly rising sea-bottom, and, being tolerably strong in itself, it prevents the perpendicular growth of the reef corals. The result is that the reef itself is driven very close to the coast. Moreover, between it and the foot of the land no deep channel can be formed by currents, for here the very hard black rock of the Andesite cliff prevents any such rapid grinding down as is easily effected in the coralline limestone. On the west coast it is otherwise. Here the currents rarely impinge directly on the face of the reef, but only at an angle. I have already shown that wherever strong currents sweep past a reef at an angle these are forced to grow perpendicularly or nearly perpendicularly upwards; this is everywhere the case on the western shore. The fact that the outer reef here is separated from the islands by a channel above forty fathoms deep and many miles wide, finds an easy and unforced explanation on the assumption of an upheaval. It is certain that the enclosed island of Babelthuap was formerly much broader than it now is, as is proved by the existence of the little island in front of Roll (see Map), which is now far from the land on the surface of the inner reef. Now, if we suppose—as we must even on the theory of a subsidence—that the island, which here consists almost entirely of tufas, originally extended nearly to the western outer reef, only narrow fringing reefs could have originally been formed on the western side; but these must from the first have grown perpendicularly, because they were impinged on by tangential currents; and since the tufa on this side could offer but a feeble resistance to the action of surface-water and rain, as well as of the surf beating on it, a small channel might soon be formed between the reef proper and the coast. This channel would presently grow wider, in proportion as the enclosed island, consisting of soft stone, was gradually eaten away, and during slow upheaval it would continue to grow deeper, in proportion as the old porous portions of the reef and the rock in

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which it was forming were more and more worn down by the combined action of boring animals and plants, and of the currents produced by the tides and by rain. Every stream has, as is well known, a natural tendency to deepen its bed; thus, while the surface currents setting directly against the reef on the eastern side prevented a perpendicular growth of the reef, and the hard rock at the base of the coral rendered the formation of a channel between the reef and the land by denudation impossible, such a process could easily be effected on the western coast by the destruction of the enclosed island, and thus the reef, forced into perpendicular growth by the tangential current, was soon at some distance from the coast.

In a similar way all the other structural features of the Pelew reefs can easily be explained by the hypothesis of a slow upheaval during their formation. It appears superfluous to discuss them here in detail, since it would involve the repetition of the same arguments as have been applied to explain the two principal points. The presence of deep channels in spots where an easily disintegrated tufa has served as the foundation for the coral built up on it, the broad and almost horizontal submarine plateau to the south of Coroere, with the narrow channels that intersect it, the large blocks of dead coral everywhere lying on the raised outer ridge of the western reef and their total absence on the eastern reefs, the gradual transition of the raised cliffs of Pelelew into the still living portion of the reef, the drying up of the channel cut by man in the eastern reef of Kriangle, and the absence of a channel on the eastern side of Babelthuap—these and many other facts are easily comprehensible if we suppose that the most important causes which determine the form of the reefs and the growth of the corals are those that I have brought into prominence, and that they are precisely such as would most easily prove effective during a period of slow upheaval.

In conclusion there are still one or two objections that must be discussed, as they are certain to be brought forward against my view. First, there is the enormous thickness attributed, according to Darwin's theory, to the reef rising abruptly from the sea-bottom; and secondly, the small depth in which only, as

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it is said, reef-building corals can exist. Nay, it even may possibly be said that my explanation as regards the Pelew reefs deserves no further attention, for the very reason that it ignores these fundamental facts, which lie at the root of the subsidence theory. I admit that I have, up to this moment, left them out of the question, but I have done so on purpose; and I must expressly contend that neither of these hypotheses deserves to be introduced into the discussion, for neither of them has been established as a fact by investigation, but is merely inferred from ill-founded observations.

With reference to the first point—the great thickness of the reef—I must confess that the method of estimating it as set forth by Darwin and Dana does not appear to me in any way to establish the conclusions arrived at. Both calculate by the same method, but with very different results; they agree in estimating the thickness of the reef on the arbitrary hypothesis that the foundation on which the submarine base of the reef rests, must have the same inclination as is visible to observation in the islands enclosed by the reef. Dana indeed assumed a somewhat less steep incline than Darwin; but it is quite possible, if not probable, that even Dana allows a too great incline for the submarine fall of the coast; for we know that even in regular cones the base usually exhibits a more gradual slope than the peak, and according to the subsidence theory it can only be the peaks of the mountains that rise above the surface of the sea; hence the base, which is covered by the reef, must probably have a much less steep incline than can here come under our direct observation. Thus, under all circumstances, the calculated thickness of the reef remains hypothetical, since it is founded on an assumption which is unproved by observation. Hence, so long as it is not demonstrated by borings that the reef is in fact as thick at its outer edge as has been estimated from the angle of inclination of the land surrounded by it, this estimated thickness cannot be regarded as an available argument for any further conclusions.

If these assertions as to the depth of the reef were actually correct, it would inevitably follow—from the fact, which hardly admits of dispute, that the reef-forming species of coral

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can live only in water of moderate depth, combined with the assumption that the whole vast thickness of the reef was formed by such shallow-water species—that such a reef could only have been formed during a period of subsidence. Of course I freely admit that the reef-building corals occur only down to a depth of twenty fathoms at most. It is consequently impossible that, during a period of upheaval, they should form a reef of more than 120 feet in perpendicular thickness. But we now know that numerous animals live at much greater depths than had hitherto been supposed. The great 'Challenger' expedition and other similar voyages have furnished proof that a very rich and peculiar fauna is universally distributed throughout the ocean, and we know, moreover, from Carpenter's investigations in the Mediterranean, that merely local causes have there prevented the development of an equally rich fauna. We may therefore infer that the constructive activity of the greater number of marine animals might very well supply materials for the formation of a solid submarine soil, even at much greater depths than those at which the true reef-forming corals are found. This probability is raised to certainty by the observations of American naturalists in the West Indian seas. Pourtalès there discovered a plateau of solid rock many miles in extent, lying at an average depth of 150 fathoms, and consisting of a compact conglomerate of fragments of shells and corals in a calcareous mud with transported rolled pebbles. This has been called the Pourtalès Plateau, after its discoverer. If this plateau were to be slowly elevated, at a rate somewhat less rapid than that required for the deposition of the new layers of solid rock, by degrees a sufficiently solid base would be raised to the level requisite for the existence of reef-building corals, and these might begin their work on the foundation prepared for them by other animals.

From all this I infer the process of reef-formation to be somewhat as follows. In the first instance, during the raising of the sea-bottom, only the foundation for the coral building would be formed, and the inclination of the plateau thus formed would certainly be very inconsiderable. Here and there channels would already be formed by the action of deep-sea currents.

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As the plateau rose to the region of reef-building corals, these channels would either become perpendicularly deeper or superficially wider, according to the force and direction of the currents acting upon them. Its tendency to grow upwards, combined with the general upheaval, would bring the highest part of the coral-stocks to the surface and so expose them to the influence of the tides as well as that of periodical or incidental rainfalls. The process will now be repeated which I have already described as ascertained by observation on separate coral-blocks; if channels have already been formed by submarine currents in the reef which has come to the surface, these will become the most natural and convenient conduits for the water flung up on to the reef; the shallows lying between the outer reef and the land, though of small extent at first, will increase, in the first instance by the outward growth of the reef, and then, in a much greater degree, by the destruction of the enclosed land; as, at the same time, the amount of water thrown over on to this inner space must increase in proportion to the increased surface, the channels must, in spite of continued upheaval, eat away the rock to a greater depth, and more or less quickly according to the nature of the rock itself.

Now, if we draw the obvious conclusions from the two antagonistic views above mentioned, all the arguments derived from observation again range themselves on my side. If it were true that thick reefs could be formed only during subsidence and exclusively by its action, we should be justified in expecting to find the same species of coral throughout the whole depth of the mass, and only the base, with a maximum thickness of about 120 feet, could under the circumstances exhibit a certain variety in the materials composing it. To my knowledge, however, no observations exist which afford grounds for this conclusion. Granting, on the contrary, that the reef was formed during a period of elevation, the inference naturally follows that the composition of such a raised reef must be heterogeneous, since in the first instance only deep-sea creatures can have established themselves on it; the reef-corals, properly so called, would in such a case form only a thin layer above the deep-sea corals. And this actually is the case, according to my personal

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observations, in the raised coral-cliffs of Pelelew. Their base, which is everywhere visible, consists entirely of a few species of *Lophoseris* mixed with other deep-sea forms; the species of *Lophoseris* belong indeed to the most delicate forms, and the genus itself is one of the most fragile of the inhabitants of the deep sea. The higher and highest portions of the Pelelew cliffs contain on the contrary only Astræidæ, Madrepores, Porites, and similar natives of small depths. And in direct proportion as this structure of the elevated Pelew reef furnishes an argument for its origin during a period of slow upheaval it affords a no less strong one against the hypothesis that it could have been formed during a period of subsidence.

Thus we have reached the end of our enquiry. It has shown us that the subsidence theory [107] is insufficient to explain the structure of the Pelew reef, and also that all difficulties disappear if we assume that the really efficient influences which have determined the growth of the corals in certain directions operated during a period of slow upheaval. And finally, it has offered a last, grand example of those direct effects of water in motion on the mode of growth of animals, of which, in a former section, I have mentioned other less conspicuous instances.

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CHAPTER IX

CURRENTS, VIEWED AS A MEANS OF EXTENDING OR HINDERING THE DISTRIBUTION OF SPECIES

ALL the parasites that live within other animals are without exception adapted to more or less extensive migrations if they are to maintain their existence as a species in the struggle for existence. If, for instance, a Trichina were incapable of living in the stomach of any other animal than man, it would have a bad chance of living any longer than the man in whom it had accidentally originated; for since its progeny imbed themselves in the muscles of the individual in whose stomach the parent produces them, any transmission to another individual, and consequently its continuance as a species, could only be secured by cannibalism. If an ordinary fluke (Distoma) were obliged to complete the whole cycle of its development in one and the same individual, it would necessarily perish with the death of its host. Thus migration is one—and in fact the most important—of the conditions of life for all Entoparasites.

On the other hand we know that this rule, indispensable to parasites, is not directly applicable to all other animals. Many, on the contrary, continue to exist within very limited and narrow regions; most of the land mollusca of small islands, for instance, have a very narrow range, and it would appear as though their continuance as distinct species for very long periods were secured by the maintenance of the balance between themselves and the external conditions of life in the locality they inhabit. Here migration, as a condition of existence, seems to be absolutely excluded. But between this and the former extreme there is every conceivable degree of transition, and we are there-

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fore justified in supposing that either active or passive migration is one of the chief general conditions for the existence of a species as such. For instance, all sedentary animals, as Corals, are just as dependent on migration as parasites; if we suppose that one single species of coral suddenly lost the capacity of reproduction by eggs and swimming larvæ, and only preserved the power of reproduction by buds, it would, no doubt, be able to extend itself, like a tree, in the spot it lived on, but it must nevertheless presently die out if the external conditions of its existence were considerably changed—as, for instance, by submarine volcanic action. Consequently the only means by which such a species can maintain itself as such, is the power possessed by its larvæ of migrating and transporting the species beyond the original limits of its dwelling-place, so that changes which might lead to its annihilation in its place of origin may not exterminate it, or at any rate not everywhere at once. The same is the case for the greater number of animals; the tendency to migrate is an important—perhaps even the most important—means employed by Nature to preserve a newly originated species from destruction.

This migration, which would seem to be indispensable to the great majority of animals, may be either passive or active. To the latter category belong the migrations of birds, of certain mammals, of many fishes, insects, &c., while many animals living in the sea are, on the contrary, passively migratory, as Salpæ, Medusæ, Pyrosomæ, &c. These are borne involuntarily by currents, while the former determine the direction of their wanderings by their own choice. In all cases of passive migration it is self-evident that the existence and distribution of the species will depend on the strength and direction of currents; but even in the journeys made by those creatures whose migrations are voluntary, the same influence is often more or less recognisable.

The effects of currents in water or in the air may be of two different kinds. In the first place they may serve as means for the distribution of the species; secondly as limits hindering their extension. We shall now consider the effects of currents in each of these directions; but at the same time it must never be

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forgotten that the results thus produced may easily be altogether concealed, or even completely nullified and reversed, by the simultaneous operation of other conditions of existence which are inseparably united with this, the only factor we have immediately to consider. Granting that a species, be it what it may, were borne by a marine current to an uninhabited island, its existence would depend not merely on its safe arrival there, but also on the favourable or unfavourable circumstances prevailing in the island. It is beyond a doubt that very many larvæ of marine creatures are carried by currents to the shore or into the mouths of rivers; but most of them perish because they do not there find suitable conditions of existence. The warm Mozambique current carries many warm-water animals out of the Indian Ocean into latitudes in which they cannot continue to live because they are unable to accommodate themselves to the low temperature prevailing there. In such researches we are obliged, and indeed required, to separate the different influences to which animals are exposed; still we must not forget that such a separation never occurs in nature, but that, on the contrary, different and often antagonistic forces are frequently quite inseparable.

1. Currents and Winds as a means of the diffusion of species.—It is a well-known fact that regular winds, as well as storms, are able to carry many flying creatures to enormous distances from their homes. Insects of all kinds are often caught hundreds of miles from the nearest land, out on the high seas; North American birds not unfrequently come across the Atlantic Ocean to Scotland; it is well-known, too, that the birds of many small islands are identical with, or very nearly related to, those of the nearest continent from which the winds blow that usually sweep over those islands. Ocean currents act in the same manner; all free-swimming or even drifting animals and larvæ are borne along by them, and the edge of the currents often marks a very sharply defined line of limitation between two quite dissimilar faunas. I shall never forget the impression made on my mind, when I was sailing round the Cape of Good Hope, by a sudden change in the fauna of the ocean surface from this very cause. West of the meridian of Cape Town the

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animal world was remarkably poor in species, and more particularly was it devoid of all the larger forms, as Medusæ, swimming Polyps, Ascidians, and such like; quite suddenly the ocean teemed with abundant life as we entered on the warm Mozambique current to the east of the Cape. The whole sea was literally covered with animals of every kind, and for more than two days we sailed without interruption through fields of gigantic Pyrosomata (*P. giganteum*, see fig. 71), which swam so close together that at night the whole ocean, out to the farthest horizon, shone with their blue gleam as if in broad moonlight.

Now we might easily be led to suppose that the winds must act exclusively on flying or land animals, and currents, on the other hand, exclusively on creatures living in the water. But

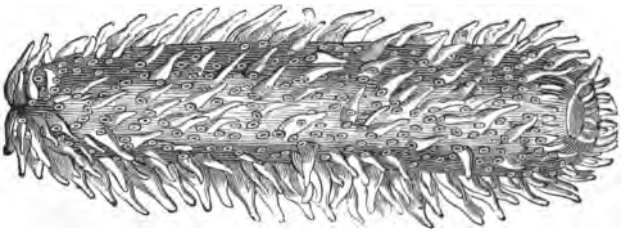

FIG. 71.—*Pyrosoma gigas.*

the investigation of certain special cases will prove, on the contrary, that these influences are often combined, so that land animals or air-breathers become dependent on currents in water, and also aquatic animals on the winds. It is nevertheless my intention to consider the action and effects of winds and currents separately.

(a) Currents as a means of distribution.—By far the greater number of invertebrate animals freely swimming or floating in water are incapable of offering any resistance to the current, and are therefore carried along in the direction which the current itself takes. All the larvæ of Sponges, Polyps, Annelida, Tunicata, Echinodermata, and very many Mollusca as well as fully-grown Radiolariæ, the floating Tunicata, Pteropoda, Heteropoda, many Annelida, and the Medusæ, though many of these are provided with special swimming organs, are

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perfectly incapable of swimming against the feeblest stream. The only invertebrate animals which are able to overcome perhaps the strongest currents are the Cuttle fishes.

The well-known wealth of forms in the Mediterranean and in the Red Sea owes its origin, certainly in great part, to the action of the constant marine currents. Both these seas are connected with the ocean only by narrow straits through which a superficial current incessantly flows in. The strength of these currents may vary with the time of year and the direction of the prevailing winds, but their direction is invariable the whole year through. Hence all the animals drifting on or just below the surface, when once they have been carried in through these narrow straits, cannot easily get back to the open ocean, and so all the forms that never sink below a certain inconsiderable depth must remain in the inland sea, and only those few species or individuals which reach the deeper return current and do not leave it can be in a position to be borne back by it to the ocean. Consequently both these seas, by reason of the inflowing surface currents, are a sort of trap; everything can get in, but nothing can get out again; thus it is inevitable—and it is actually the case—that a vast accumulation of species as well as of individuals occurs in these seas, wherever the other necessary conditions for the existence of the individual forms exist.

Another result which may be directly referred to marine currents—in combination, of course, with other influences—is the wide distribution of such marine animals as have free-swimming larvæ. If, for instance, we compare the marine mollusca of the Red Sea with those of the Philippines, their extensive resemblance strikes us at once; nay, even those of the Western Pacific closely agree with them both in several respects. In strong contrast with this state of things is the fact that the land mollusca of Eastern Africa, the Moluccas, the Philippines, and western islands of the Pacific, exhibit scarcely a single genus which is common to them all, and the species—irrespective of a few unimportant forms probably introduced by man—are totally different in all these provinces.

This resemblance between the fauna of extensive marine

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districts proves at once that the constant currents acting in these regions have prevented the separation of the varieties that probably occur, into distinct species; for we know from Darwin, that a new species can never be in a position to maintain itself unmixed, if the individuals which have been modified by some influence are not prevented from breeding in again with the parent stock. But the currents which keep the Indian Ocean and Red Sea in communication with the Pacific Ocean, being constant, can just as well transport the parent forms as the varieties, and consequently a free crossing between all the forms derived from one stock is not only facilitated but rendered

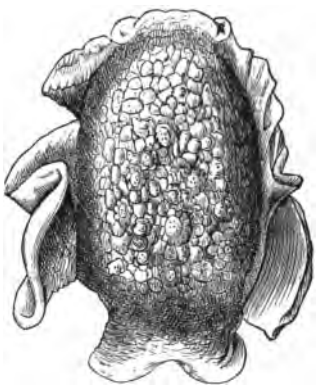

FIG. 72.—*Onchidium tonganum*, natural size.

inevitable. The Crustacea and Fishes of the Red Sea correspond very exactly with those of the Indian Ocean and Philippine Sea; more than half the genera and a large number of the species are actually identical in these two very widely remote regions. Even species which have accommodated themselves to a quite peculiar mode of life are sometimes dispersed throughout these regions; thus, for instance, the *Cryptochirus* of the Red Sea appears to be in no respect specifically different from that of the Philippines, and the *Hapalocarcinus* of the Pacific, described by Stimpson, is found, it would seem identical in species, at the Isle of Bourbon not far from Africa. *Onchidium verrucula-*

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tum, a land mollusc living on the seashore, and having a very peculiar mode of life and anatomical structure, is found absolutely identical in the Red Sea, the Philippines, and North Australia, and on the Chinese and Japanese coasts. Another species of the same genus, *Onchidium tonganum* (see fig. 72), is found alike in the Tonga Islands and the Mauritius. Different species of the genera *Auricula* and *Scarabus*, belonging to the Pulmonata, of which the larvæ have an operculum and probably float in the sea, have an equally wide distribution. All these, and many other species which cannot be mentioned here, are easily transported by currents, either in the larva state or fully grown, and the general similarity I have indicated of the marine fauna, from the Red Sea as far as the western half of the Pacific, must be the result of a diffusion of species effected by constant marine currents.

The influence of such currents is even more conspicuous in the distribution of many land-animals, although at first sight it might seem paradoxical to say that the distribution of animals living on land can be affected by currents in the sea. The evidence, however, is easily produced. If we reflect, to begin with, that all Land mollusca, the great majority of Insects, and many Reptiles and Birds, being vegetable-feeders, are directly dependent for their existence on certain species of plants, it is evident that their presence in particular spots, as well as their geographical distribution, depends in the most direct manner on the action of currents, since these it is which principally determine the distribution of the plants on which they feed. Granting that a monophagous insect were by any means transported to an island where it did not find the only plant adapted for its support and to which that plant never could be brought even by currents, that species must inevitably perish. But there is yet another way in which currents may affect the distribution of animals, besides this indirect mode by means of the plants they feed on. Many Insects are easily transported as larvæ, in and on floated trees and wood; small Mammals, no doubt, are also carried in this way from one place to another; the same is the case with many Reptiles and Amphibia, and it is more than probable that land-snails can travel only in this way, and in no other,

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from one island to another. We may therefore expect to find on islands in the neighbourhood of a continent a terrestrial fauna closely resembling that of the continent, if the marine currents are such as to favour transport from the mainland to the island. Examples abound: the Galapagos have a South American fauna, the Sandwich Islands a North American one. Moreover, the terrestrial fauna of an island may be expected to be very dissimilar from that of the nearest mainland when it does not lie within the influence of the currents flowing from it. Of this too there are plenty of examples; the best known is the case of the Canary Islands; their land mollusca have a pronounced European character, although by their geographical position they belong rather to Africa than to Europe. Attempts have been made to explain this fact by an assumption that there was formerly a connection between these islands and Europe through Spain; an assumption which might certainly find much to support it, if animals so large as to be incapable of being transported by winds or currents, had been found in these islands, either living or fossil. This, however, is not the case, and it appears to me that the force and direction of the currents sweeping past these islands amply suffice to explain the European character of the land mollusca and insects of the Canaries.

Supposing that a long chain of islands had connected two lands lying far apart and differing widely in their fauna, it might be expected, and with great probability, that the fauna of this group could have retained no special homogeneous character. For the vicinity of the two terminal countries, and the currents probably existing, might easily have caused on the islands a mixture of the two dissimilar faunas. This is, in fact, sometimes the case. The Philippines lie very nearly north and south; the northern islands are connected with China by the Bashees and Formosa, while the southernmost island, Mindanao, is connected by Celebes and some smaller islands with the Moluccas, and the south-western island, Palawan, hangs on to Borneo by Balabac. Wallace certainly includes the Philippines with China; the Malayan peninsula, Sumatra, Java, and Borneo, with some smaller islands, constitute his 'Malayan province,' which he contrasts strongly with that of New Guinea and Australia, to

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which he adds the Moluccas and Celebes. But quite irrespective of the question thus raised, which I shall discuss presently, the different portions of this Malayan province exhibit great and extraordinary differences. A greater contrast can hardly be conceived of, than that, for instance, between the fauna of Hong Kong, Amoy, or even Siam, on one side, and Borneo, Java, and Sumatra, on the other. And this difference is repeated in a very striking manner in the Philippines, where the northern district displays an unmistakable harmony with the true Chinese fauna, while the southern islands show a marked resemblance partly to Borneo, partly to Celebes and Gilolo, and partly to the western islands of the Australian region.

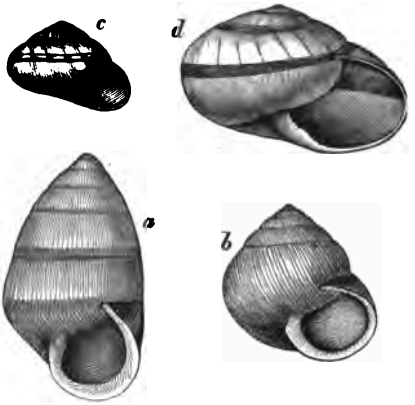

FIG. 73.—Shells of Molluscs from the Philippines. *a*, *Cochlostyla stabilis*, Sow.; *b*, *Chlorœa* n. sp.; *c*, *Chlorœa benguetensis*, S.; *d*, *Cochlostyla magtanensis*, S.

As these remarkable facts are probably not universally known, I will here give rather fuller details as to the more important of them.

The most prominent feature of the fauna of the Philippines is beyond a doubt its terrestrial mollusca.[108] Setting aside the minuter forms for the present, the following five genera are those which give this fauna its peculiar character: *Cochlostyla*, (see fig. 73, *a* and *d*), *Obbina*, *Chlorœa*, *Helicarion*, and *Rhysota*. They are here extremely rich in species, while on the adjacent islands, not belonging to the Philippine group, only a few quite

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distinct species occur which can be included in these genera. Thus three species found in Borneo belong to the genus *Cochlostyla* (*antiqua*, *sulcocincta*, and *xanthostoma*). *Chloræa* (see fig. 73, *b c*) is entirely confined to the Philippines, and is not found even in Mindanao; *Helicarion* also is a purely Philippine genus, and its nearest allies even do not occur in India, as might be expected from Wallace, but in the Australian region; of the genus *Obbina* four species belong to the Australian province and one to Borneo; *Rhysota* is confined to the Philippines. Associated with these peculiar forms are other genera which are not characteristic of these islands, and which have a very remarkable geographical distribution. Closely related to *Chloræa*—in anatomical structure, though not in the appearance of

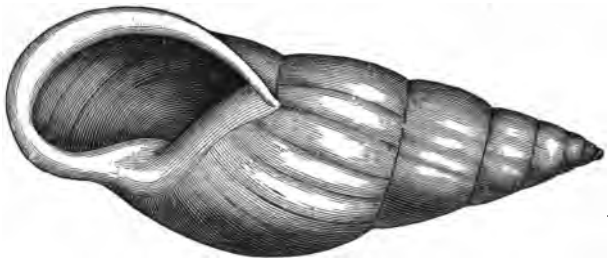

FIG. 74.—*Amphidromus maculiferus*, SOW.

the shell—is the widely diffused group of *Helix similaris*, which is very common throughout the China region; three or four species occur in the north of Luzon, and only one extends as far south as Bohol; none at all are found in Mindanao. The only Philippine species of the genus *Clausilia* inhabits the island of Camiguin to the north of Luzon; it belongs to a Chinese division of this widely distributed and highly variable family. *Chloræa* itself is most extensively developed in the north of Luzon. Thus these three genera give to the fauna of the northern Philippines a sprinkling, as I may say, of the Chinese.

At the extreme south, on the other hand, there is a certain harmony with the fauna of the Moluccas and the Malayan peninsula. For instance, the genus *Amphidromus*, which is so characteristic of the Malayan province (see fig. 74), sends only

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two species to Mindanao, of which one (*A. maculiferus*) extends as far as Bohol and the south coast of Leyte, while the other (*A. chloris*) is found only on the south-west point of Mindanao. Three species of the genus *Xesta*, which is at least equally characteristic of the Malayan islands and even of India itself, as the two species of Amphidromus above mentioned, have the same distribution; two of them have hitherto only been found in Mindanao (*X. Antonii* and *nobilis*), the third (*X. Cumingi*) lives in Mindanao, Camiguin de Mindanao, and Bohol; and since, moreover, the number of typical Philippine species is very inconsiderable in Mindanao compared with the others, the remarkable encroachment of Indian forms on the south Philippine province is all the more conspicuous.

Hence, having regard to these differences, the Philippines may be divided into three regions: I. The northern, which exhibits in some degree the Chinese character. II. The southern, which has Malayan or Australian affinities. III. The Median, which may be called typically Philippine, since it has scarcely any admixture of foreign elements. This result is confirmed when we come to consider the other animals in the islands. The stag of the Philippines has, so far as I know, hitherto been found only in the north of the archipelago, and its nearest allies are in China. *Galeopithecus* and *Tarsius*, both highly characteristic of the Indian Islands, only occur in the southern Philippines, and never in Luzon; an apparently new species of the Malayan genus *Cladobates* is found only in Mindanao. One single species of *Barbus*, a fish, I found only in Mindanao; this genus is represented in the Malayan islands by very numerous species; and the singular *Platyptera aspro*, of the family of Gobioïdæ, in the same way occurs only in the south of the Philippines. Among reptiles, *Amblycephalus boa*, *Dipsas dendrophila*, *Tropidophorus Grayi*, and *Ptychozoon homalocephalum*, all living exclusively in Mindanao, belong to the purely Indian fauna. The same mixture of autochthonous species with Indian species in the south, and Chinese in the north, is displayed by the butterflies, as my brother, George Semper, informs me, from studying my collection of insects.

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This mixture of the true Philippine fauna with the two foreign elements at the opposite ends of this chain of islands can, as it seems to me, be satisfactorily accounted for only by the assumption that the marine currents, which in those seas are dependent on the monsoons—or at any rate are greatly influenced by them—have been the essential means of transporting animal forms.[109] For animals from China could by their aid reach only the most northern islands, while those from the Indian and Australian islands must first reach Palawan and Mindanao. This, as I have shown, is precisely the case; and the almost entire absence of such forms, which would easily betray their foreign origin, from the middle region of the group confirms the idea that in the north immigration has taken place from the west and in the south from still farther south.

The general conclusion to be drawn from this—*i.e.*, that the constant currents combined with the changes of the monsoons have been the principal agents in the peculiar distribution of many of the land mollusca of the Philippines—is still further strengthened by the following considerations. If land-snails in general can be conveyed from one island to another at all, it certainly can only be by currents, and presumably by the intervention of trees on which they are borne, and their eggs may be transported in the same manner. But it is self-evident that in this way a selection will be effected between the different forms, according as they are qualified to endure an ocean voyage or not. Large species and such as live in the highest branches of trees and lay their eggs there, like all the species of *Cochlostyla*, are obviously far more difficult to transport than small species which can creep into the rifts in trees or between the roots; the species of a group which, like *Helix similaris*, live on the ground among stones and earth, will be almost as well protected on the sea-voyage as the operculated snails which have the mouth of the shell closed by a lid or shield, which protects the soft part of the creature almost perfectly from contact with the salt water. Hence we may expect to find in islands a greater multitude of different species in those genera which are most easily transportable. We know that the constant introduction of the parent forms in any numbers into a new colony will prevent the

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formation of a new species in that spot. But the difficulty of transport across the sea must, on the contrary, probably prevent the frequent importation of new individuals of the parent form, and consequently the formation of a new species will be facilitated by the impediment thus offered to free crossing with the original form.

These inferences from the view that constant currents constitute an important auxiliary in the diffusion of land mollusca are, as every conchologist knows, in perfect accordance with the facts. Most of the small species and of the operculated species have a much wider range than the large inoperculated forms. While the typical Philippine genera *Cochlostyla*, *Rhysota*, *Helicarion*, *Chloræa*, and *Obbina*, which principally dwell in trees, are found only, or almost only, in the Philippines, the small genera, as *Subulina*, *Trochomorpha*, and *Ennea*, among the Helicidæ, and the Operculata *Cyclophorus*, *Alycæus*, *Helicina*,

FIG. 75.—*Trochomorpha* eq.

and *Diplommatina*, have a very wide distribution, and at the same time a remarkable uniformity of species. Thus *Ennea bicolor* ranges from India to the Pacific Ocean, where I myself found it in the Pelew Islands; the same species of *Helicina*, *Pupina*, and *Leptopoma* occur in almost all the islands of the Philippine Archipelago, while, notwithstanding the great number of species in the genus *Cochlostyla*, no two identical forms are to be found in Mindanao and Luzon. The species of the genus *Trochomorpha* are extremely similar in appearance, whether they come from India, the Moluccas, the Philippines, or the islands of the Pacific; nay, several species of this genus are distributed throughout this vast region, almost without any variation in their shells.

In the closest connection with these facts is the theory, which, under the name of the Migration theory—or, as it is now called, the Separation theory—has been propounded by its originator Moritz Wagner in opposition to Darwin's theory of selec-

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tion. Its principal propositions are as follows: The struggle for existence and the selection it gives rise to cannot by itself lead to the formation of new species; this can only take place when, in the first place, one or a few specimens of a species are introduced at a variable stage into a new home; when, secondly, these by their removal to a distance are prevented from cross-breeding with typical individuals of the parent stock; and when, thirdly, a selection is effected by the external conditions of existence among the varieties arising in the new colony.[110]

Setting aside, for the moment, the question as to whether this theory is really opposed to Darwin's or no, we will in the first place inquire whether in its strict application it is actually capable of explaining all the facts occurring in nature. And I must at once confess that in this respect I can by no means admit Wagner to be right.

Many kinds of Infusoria are distributed over the whole globe in sharply defined species. Now it is quite certain that among these creatures no separation by removal exists to prevent the free interbreeding of any variety with the parent form. They are most easily transportable, either living in water, or when dry, as dust by the wind, and indeed we see that in no other animal group are there species so cosmopolitan and so universally distributed as among the Infusoria; nevertheless the characters of the different species remain very constant. Between the tropics there is no sharply demarcated breeding period for the greater number of marine animals, so that fully grown individuals, young ones, and eggs, can at all times be found side by side in every stage of development. Moreover the fertilisation of the eggs is effected while they are freely swimming in the ocean in the case of almost all Echinodermata, all Cœlenterata, many worms, most bivalves, and many Tunicata, Brachiopoda, and Bryozoa; and in the few viviparous forms of these groups no union of the sexes takes place. On the contrary, the fertilisation of the ova is left to chance; the spermatozoa or male element being expelled into the sea and conveyed by currents which bring them into contact with the eggs or with the female parent organism. In these and also in all those marine species which have free-swimming

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larvæ, absolute separation of all new varieties from the parent species is thus rendered impossible. Nevertheless, these forms have specific peculiarities as distinctly marked as those of insects, vertebrata, and land mollusca, the only animals which Wagner takes into consideration in his investigations. According to his theory, on the contrary, all such species, whose free crossing with the parent form is not prevented by separation, should remain very variable, and should not be distinguishable into any great number of well-defined species. But, this not being the case with the creatures above mentioned, it follows that separation by distance cannot be, as Wagner asserts, the one exclusive cause of the origin of new species.

It is admitted, of course, that Wagner in his argument recognises the influence of the external conditions of existence and duly allows for them; but since these occasionally act as a selective power—as in the case of many lower marine animals—without the co-operation of a contemporaneous separation of the varieties from the parent form, this last circumstance can never be the sole cause of the process of forming a species, though it may sometimes bear a principal part in it. The first question is thus answered.

The second question is: Is it indeed the fact that Wagner's separation theory differs so totally from Darwin's theory of selection that each completely excludes the other, as Wagner seems to think? It does not appear so to me. Both assume that different species are more or less variable; both assert that free crossing with the parent form must be prevented if a new species with constant characters is to be developed; they agree in believing that a selection also must be effected among those variable forms in order to induce the constancy of specific characters and to increase the useful ones by accumulation. I can detect only two trifling differences in their respective views. Wagner appears to think that physical separation or removal, which certainly is a very frequent result of migration, is the means exclusively employed by nature to prevent free crossing, while Darwin says that this result may often be effected by numerous other and very dissimilar causes, as for instance by differences in the size of the male and female indi-

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viduals, by antipathy and sympathy, by incompatible differences of structural character, &c. Actual separation, which is often but not exclusively the result of migration, may no doubt sometimes prove a stronger means of preventing free crossing than such physical or structural peculiarities, but it cannot possibly be disputed that these, in many cases, certainly suffice to effect the same result as, in other cases, is brought about by Wagner's favourite means, local separation. Hence, Wagner's theory lays far too much stress on migration as a factor, so far as regards the indispensable prevention of crossing, and altogether ignores others which, under some circumstances, are of quite equal efficiency. Consequently migration must be put in the same category with all the other causes which, according to Darwin, may interfere to prevent cross-breeding; and so Wagner's theory forms in fact a subsidiary to Darwin's.

The second apparent difference between their views seems to lie in the method by which the selection between the different varieties takes place. Darwin says that it is 'the struggle for existence,' while Wagner vehemently quarrels with this expression and regards the influence of external surroundings as the sole efficient means—the influence, that is, of the conditions of existence. At the first glance this might appear to be a fundamental difference; but the difference in the expressions used is altogether superficial and may have arisen merely from a misunderstanding of the word used by Darwin. Wagner expressly says, in his latest work, in terms that cannot be misunderstood, that he is of opinion that the words 'Struggle for Existence' * are used by Darwin to denote exclusively that direct combat between two individuals of the same species in their efforts to possess themselves of the same prey or of the same female.[111] This, however, seems to me a quite erroneous interpretation of Darwin's expression. For although Darwin himself frequently explains that in his opinion the personal struggle between two individuals of the same species exerts a far greater selective power than the surrounding conditions can effect with all their sudden changes, he by no means ignores

* 'Not very happily rendered into German,' says Dr. Semper himself, 'by the words, *Kampf ums Dasein*.'

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these influences, and in various places expressly states that they may sometimes have had precisely the same results[112] as Natural Selection in its most limited acceptation. In short, if I rightly understand Darwin, he applies this expression, not exclusively to the struggle or combat between two individuals, but conceives of it rather as the sum total of all the efforts which a newly constituted species must make to succeed in conquering all the hindrances to its development, and at the same time to avail itself to the utmost of every favourable circumstance that offers. It must certainly be conceded that Darwin generally applies the words 'Natural Selection' to those cases only of the most direct competition between two animals, of the same or of closely allied species. This indeed is the obvious inference from the fact that he considers it necessary to contrast *Natural* and *Sexual* Selection, although the sole difference between them properly consists in this: that in the former the struggle is for a dead object, in the latter for a living one, *i.e.* the female. It may still further be conceded, as indeed Darwin himself has admitted, that in the first instance he somewhat undervalued the selective influence exerted by the surrounding and external conditions of life; but to assert that he wholly ignored them is far from the truth. On the contrary, these influences constitute an essential part of his theory, though Darwin himself assigns them but a small and undoubtedly too limited part in it. Still Wagner's separation theory is not thereby opposed to Darwin's, but, on the contrary, an integral part of it; and it is an indisputable fact that the various propositions which constitute the 'separation theory' had long before, if in a different form, been announced in the chapter on the geographical distribution of animals in Darwin's work on the Origin of Species.

But while I must thus, in the most positive manner, dispute the idea that Wagner's theory is in any way essentially opposed to those of Darwin, I may on the other hand admit, once more, that migration and the separation frequently occasioned by it, as well as by currents, may exert a very decisive influence on the formation of species. Such an influence is recognisable in the fact that such land-snails as are difficult to transport by

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currents exhibit a great wealth of different species even in adjacent islands, while those species which are easily transported have a much wider range, combined with a greater constancy of character, than the species of the former group.

It might perhaps be inferred from the foregoing remarks that it is my view that in every case when faunas widely separated by distance exhibit a certain resemblance or affinity of species, one and the same influence, *i.e.* the action of constant marine currents, must be regarded as the cause of that correlation. But I think I hardly need guard against such a misapprehension; a brief account of the most interesting cases of this kind will suffice for my purpose.

FIG. 76.—*Temnocephala chilensis*, Blanchard, which lives, absolutely identical in species (no difference being perceptible in either the external or anatomical character), in Chili, Java, and the Philippines. Parasitical on fresh-water crabs belonging to quite different genera.

Günther has shown that the tortoises of the Mauritius [113] are very nearly related to those of the Galapagos, which, lying near South America, are almost the antipodes of the island in the Indian Ocean. The characteristic species of *Bulimus* (a land mollusc) in South America have their nearest allies, not in North America nor in the West Indies, but in New Caledonia and the Feejee Islands, as I can attest from my own minute investigation of such animals. The extinct birds of Madagascar show a near relationship to those of New Zealand; many fresh-water fish of New Zealand are identical or very nearly allied with those of Chili; *Temnocephala chilensis*, a small parasite

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(see fig. 76) on the legs of a fresh-water crab in Chili, occurs identical in species in the Philippines and in Java, but on perfectly different crabs. It would be easy to multiply instances, but these will suffice, I believe, to show that any attempt to explain them by the action of constant marine currents must altogether fail. Other causes must here have combined to produce so striking a resemblance between the faunas of islands lying so far apart; but it would be difficult to discover them in every case. Wallace has justly observed in his great work that such cases ought, under the circumstances, to be regarded as a proof of the justice of the hypothesis that those types which have occasioned the similarity of remote faunas must have had a very long historical duration, persisting very likely throughout many geological epochs. Also it must not be forgotten that the convergence or parallelism of different species may sometimes have led to the formation of two similar faunas in very remote places in modern times. This, however, is not the proper place for a discussion of this interesting point, and I must refer the reader who is particularly interested in it to the brief remarks he will find in the Appendix.[114]

(b) The wind as a means of dispersal.—It is evident that the distribution of all flying creatures, *i.e.* the selection of forms among them, must in a great degree depend on the direction and strength of atmospheric currents, whether these be regular winds or irregular storms; but it is a matter of very great difficulty to determine what share each mode of atmospheric motion may have, or how they may co-operate.

Instances of animals being carried by wind-storms far beyond the limits of their native province, or even beyond seas, are universally known, and it must here suffice to refer the reader to the chapter on the Means of Dispersal in Darwin's work, in which a great number of independent examples are given. Still we are justified in inquiring whether indeed such an accidental transportation of solitary individuals to countries where they are merely interlopers, can have often led to the acclimatisation of a species in a new country. For it must not be forgotten that, independently of the difficulty they will

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experience in maintaining themselves under the new conditions of existence, their ultimate establishment there must generally depend on two individuals of the same species and of different sexes being simultaneously, or almost simultaneously, carried to the new country. On the other hand, the strength of regular winds, such as monsoons, trade winds, &c., would not seem to be so great as that flying creatures, such as birds and insects, could be carried away by them against their will, nor, indeed, with such rapidity as would be requisite to enable them to reach some distant destination before they had perished of hunger. There are, however, a few cases in which such effects of wind are apparently so obvious that they cannot be overlooked or disputed.

The most conspicuous and often-discussed example is afforded by the fauna of the islands lying near to, or at no great distance from Africa. It has long been known that, as regards their terrestrial fauna, the Azores, Madeira, and the Canary Isles belong to Europe, and that even their birds and insects are for the most part only specifically distinct from those of Europe. Nay, Dohrn has lately shown that even the Cape de Verde Islands, which are divided from Africa only by narrow straits, belong, as to the greater number of their animals, to the European region, although a small admixture of species from the Ethiopian region can be pointed out. Wollaston, Murray, and others have attempted to explain this remarkable circumstance in the following manner. They assume that all these islands were formerly connected with Europe by the mythical Atlantis; an explanation which escapes all possibility of discussion and merely appeals to the greater or less credulity of different inquirers. The explanation offered by Wallace in his latest work is founded, on the contrary, on forces of which we can accurately estimate the efficiency, and it seems to me that his views are amply supported by their extreme probability. He points out that in this region of the Atlantic, steady winds and storms alike blow in the direction which would be required to allow of such atmospheric currents having transported European animals to these islands. As an indirect argument for the correctness of this view he adduces the total absence of all land

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Mammalia and Reptiles from the Cape de Verde islands, which would be incomprehensible if they had formerly been in actual connection with the European continent; and as a direct proof he adduces the fact that almost all the birds are of European species, and that all the European species of insects which are found on these islands are strong flyers, while, on the other hand, 45 per cent. of the indigenous species of insects cannot fly at all, being in fact wingless. He has still further considerably strengthened his views by an investigation of the peculiarities exhibited by the land mollusca of these islands. These, as I have already said on the strength of Dohrn's researches, bear a typical European character, but not one species is identical with a European form. The most important means of transport for land Mollusca are, beyond a doubt, marine currents; the possibility of eggs being conveyed by adhering to the feet of birds does not here come under consideration. The direction of the currents in the Atlantic is, moreover, such that the conveyance of European land-snails to these islands might easily be possible. But it is evident that constant winds would be able to transport a much greater number of individual flying creatures within a given time than that of the land mollusca conveyed by currents. Hence these last would exhibit a considerably less variety of species than the former; for we know that the greater facility for free crossing with the parent species renders the formation of new species more difficult, while it is facilitated when a variable species that has been introduced into a new home is by any means prevented from constant inbreeding with the parent form. And this is directly applicable to these islands; there is no serious hindrance to the transport to them of flying creatures from Europe in great numbers, and accordingly we see that the good flyers among the insects of the Canary Islands are almost all identical with European species; and it is in perfect agreement with this that the land mollusca which are difficult of transport have become differentiated into a number of new forms, since the greater difficulty of immigration has prevented the crossing of these varieties with new individuals of the parent stock.

This, of course, presupposes, or, rather, it follows from the

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foregoing remarks, that the direction taken by the migrations of flying animals is, in a great measure, determined by the direction of the winds; without this, Wallace's explanation would remain as unsatisfactory as the hypothesis of the sunken Atlantis. Such effects ought, as we may suppose, to be most easily recognisable in the migration of those flyers which of their own free will make long migratory and aerial journeys; moreover, we might expect to find some reliable data in observations made on migratory birds. But, strangely enough, all the investigators of the phenomena of migration in birds appear to have taken no notice of this matter; my closest researches have failed to find any data with regard to it, and the only remark which may have some value is that of Von Brehm, that migratory birds always fly against the wind. The necessity for this is self-evident; a bird which is driven before even a moderately strong wind blowing through its feathers, is prevented flying, and still more hindered in steering. Even in the most recent and very thorough researches as to the phenomena of the migrations of birds by Von Palmén,[115] this point is wholly disregarded, and though it must be admitted that several of the lines of migration laid down by him from many observations can by no means be brought into agreement with those of prevailing winds, on the other hand the number of cases is not small in which a very extensive agreement between the two is conspicuous; this is the case, to cite a single example, in the west of Europe.

If then the observations at our disposal afford no satisfactory information as to the question how far the influence, certainly exerted by the wind, affects migratory animals, it is still more difficult to trace its effects on aquatic animals, notwithstanding that they undoubtedly come under its influence. This influence can naturally only be effective in two ways, either by flying creatures, like water-birds, carrying small animals or eggs on their journeys with them, clinging to their feet, or by the wind transporting these aquatic creatures directly through the air. Darwin has pointed out the possibility of the first mode in his discussion on the geographical distribution of fresh-water mollusca, particularly with a view to explaining the fact, recognised by him, that these animals,

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unlike their congeners living on land, display an extraordinary range of identical species. Eggs or young individuals, so he argues, might make very long journeys adhering to the webbed feet of a migratory duck; and as such journeys must be frequently repeated, according to the constant direction of the migrations or circuits of the bird, numerous specimens of the same species of water-mollusc must traverse the same route. The accumulation of individuals of the parent species in the same colony thus caused would prevent the formation of a new species, since the selective influence of the struggle for existence in the new conditions of life would be constantly counteracted by the repeated immigration of individuals of the parent form.

This explanation is satisfactory, and in many cases it certainly seems to be the right one, as, for instance, in the case of the distribution of the European fresh-water mollusca. Still very considerable difficulties stand in the way of its extensive application. It must, in the first place, be observed that the great similarity of the fresh-water mollusca throughout the globe, assumed by Darwin, does not exist to such an extent as might be supposed from what he says. This contradiction on my part requires some explicit verification. The genus *Unio*, for instance, is distributed almost everywhere on the face of the globe; it is absent only from a few tropical countries, as the Moluccas, the islands of the Pacific, probably New Guinea, and others; but the species of Unio are extraordinarily various; in North America almost every little stream has its own peculiar form, and the European, Asiatic, and Australian species are widely dissimilar. These differences may be even greater and more striking than we now suppose, for we have hardly exact knowledge enough of the organic characters of more than a few dozen forms to venture to pronounce a decisive opinion, while hundreds of species are as yet known to us only by their shells. The other genus of fresh-water mussels, *Anodonta*, has an even wider range, for it occurs even in those islands where Unio is wanting. But for this genus also these remarks hold good. Among the Univalves the genera *Melania* and *Paludina* (fig. 77) have a very wide distribution, and exhibit a considerable resemblance in the

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characters of their shells; nevertheless, both have been subdivided into a great number of different genera, and, as has been proved by a study of the animals themselves, in many cases this has been perfectly justified. But hitherto we do not know the anatomy of more than a few dozen of these genera, and so it is at least possible, if not probable, that a more exact investigation of the animals may demonstrate precisely the reverse of any extensive uniformity in the structure of the species placed in these genera. Thus we have no longer the right to speak of the extensive distribution of the genera *Melania*, *Paludina*, *Anodonta*, and *Unio*, and it is consequently superfluous to

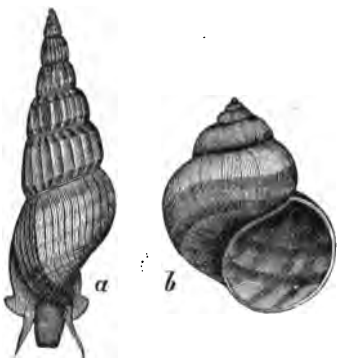

FIG. 77.—Two operculated fresh-water univalves. *a*, *Melania*; *b*, *Paludina*.

seek an explanation of a fact which, though it cannot be shown to be false, is as yet 'not proven,' but, on the contrary, cannot be brought into harmony with the few facts which are ascertained and established.

One more difficulty must here be briefly alluded to. According to Darwin's views it might be expected that all easily transportable kinds should show a greater uniformity of species than those which are less protected against the perils of a long journey. But the reverse is often the case with fresh-water univalves. The species of Paludina and Melania have an operculum which fits almost exactly into the mouth of the shell, so that the animal would seem to be effectually protected;

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but the species of *Limnæa*, *Planorbis*, *Physa*, and *Succinea*, which also live in fresh water (see fig. 78), have no such protection, and the mouth of the shell is remarkably large. Research has shown that, as a fact, operculated snails resist injurious influences far more successfully than those without an operculum. According to this the species of the inoperculated fresh-water univalves ought to exhibit a much sharper differentiation into separate species according to their habitat than the

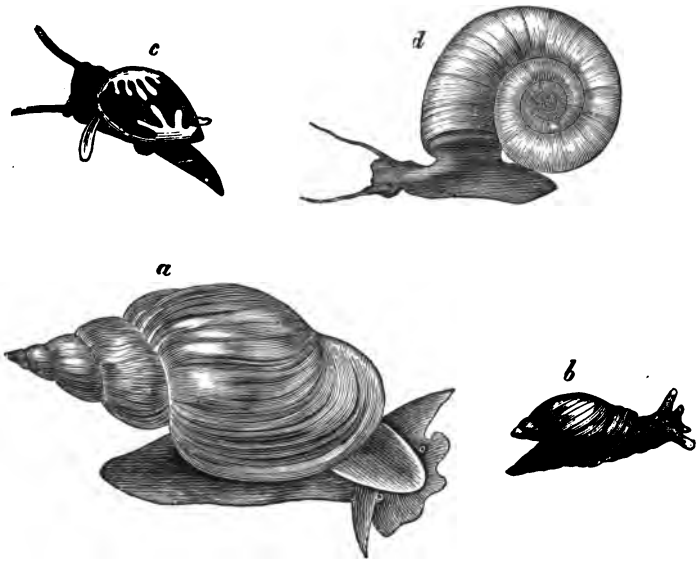

FIG. 78.—Various fresh-water snails. *a*, *Limnæa*; *b*, *Succinea*; *c*, *Physa*; *d*, *Planorbis*.

operculated forms; but the fact is precisely the contrary. Analogous examples of other fresh-water animals could easily be adduced. Thus, for instance, it is impossible to explain the existence of *Temnocephala chilensis* (see fig. 76) in Chili, the Philippines, and Java, by supposing it to have been carried thither by birds, for it deposits its eggs in its host; and these are creatures much too large to have been carried alive by birds across the ocean.

It would certainly be, I will not say a grateful, but a very

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important task to determine the share which can with any certainty be ascribed to the effects of atmospheric agency in the transportation of fresh-water animals. At present we cannot do this even approximately. The investigation would be uncommonly difficult, for, in order to get a clear idea of it, it would be necessary to contemplate at the same time the questions, first: Whether many nearly-allied forms, or forms which to our eye appear as identical, might not have originated in two or more distinct localities by what is known as polyphyletic descent, and secondly: How old the different forms may be historically in the development of the animal world. In every case we should thus be led to an exact inquiry into the genealogical affinities of the animal. One example will suffice. True Astacidæ or river cray-fish occur in Europe, in America, and Australia, while they are absent from the intervening countries and islands. Now, it would certainly be more than bold to derive either of these groups directly from one of the others by any theory of transportation through the air on the feet of water-birds; consequently the question at once arises, whether we here have an instance of polyphyletic descent or not. Now, so far as is known, there is no Crustacean living on land or in fresh water, in either of the three continents, which can be regarded as the parent stock of the Astacidæ living there. But in the different Oceans we do indeed find crustaceans—as, for example, the species of *Paranephrops*—which have been considered as the nearest allies of the river crustaceans; we will not here discuss whether with justice or no. Now, if these different marine Astacidæ had gone through the same migrations into rivers or on land, independently of each other in the three continents, and had passed through analogous modifications corresponding to those migrations, the extraordinary resemblance of the river Astacidæ at such wide distances from each other would be satisfactorily explained. But this method of explanation obviously presupposes that our views as to the essential affinity of the animals in question must be in fact perfectly accurate.[116]

Though, in the instances we have thus far been considering, it has been difficult, or even almost impossible, to point out the

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effects of wind on the migrations of fresh-water animals, there are other cases in which they can be recognised with the greatest ease. We know that our atmosphere is densely full of the desiccated germs of minute organisms which are most easily raised and borne by the wind, but which fall to the ground as soon as the air is still again. We have learned from the highly important experiments made by Tyndall on lower organisms and their distribution, that the only unfailing method of freeing the air of such microscopic elements is absolute stillness. Thus, if it were possible to trace with any certainty this sediment of the atmosphere, so to speak, we should be in a position to determine the direction which the different animals occurring in it must have taken through the air.

But two conditions must be fulfilled in order that the distribution of animals may thus be effected: In the first place, the

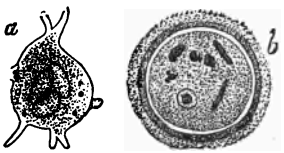

FIG. 79.—*a*, An Amœba in its plastic state, with small powers of resistance; *b*, the same encysted, *i.e.* enclosed in an envelope which protects it against injurious influences.

force of the air in motion must suffice to raise the organisms high up; and, secondly, the organisms themselves must be capable of enduring the associated desiccation. These conditions are in fact fulfilled, but only with microscopic animals and the eggs of minute Invertebrata. All Infusoria, for instance, have the power of enclosing their soft bodies in a firm envelope, the cyst (see fig. 79); this they do regularly before reproduction or whenever the external conditions are too unfavourable. In this encysted state they are able to endure desiccation without any injury to their vitality, and, what is more, they can lie dry for years—how long is not known—and then, after tens or perhaps even thousands of years, revive to a new life. In this state, being extremely light, they are naturally easy to transport, and it will therefore not surprise the reader to hear that Ehrenberg was able to detect, in dust collected in Germany at certain seasons,

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minute organisms of this class which demonstrably belong to the West Indian fauna. The only possible explanation of this fact is the assumption that these organisms were borne to us by the higher stratum of the returning trade-wind and deposited in Europe, where the trade-wind gradually sinks. In the same way all those higher organisms are capable of being conveyed through the air which I spoke of in a former chapter as being able to endure long periods of desiccation: the Tardigrada, the Rotatoria, and the eggs of various small Crustacea and Worms.

If, in fact, the wind in this way fulfils the function of distributing such organisms, all such passively migratory creatures must exhibit a very wide range; or else—which is the same thing—a great uniformity must prevail in the fauna of different countries as regards these forms, since the extreme facilities afforded to the migrated individuals for constant crossing with those of the parent species which are subsequently introduced, will easily prevent the rapid formation of new species in the new locality. The facts, so far as they are known, agree to a certain extent with these hypotheses; but it is impossible at present to venture to offer any decided opinion in the matter; the gaps are still too great in our knowledge of the distribution of these animals, the only creatures which for the moment concern us. We, as zoologists, may perhaps be blamed for this, since it is our duty to collect the observations bearing on the question; but such a reproach does not touch us very deeply. Each science must determine its own course without regard to any collateral outside interest, and it may even occur that important questions should be for the time set aside from absolute necessity, if, within the province of the special science to which they appertain, no key as yet exists to their solution. And this is at present, or has hitherto been, in a conspicuous degree, the case with the point under discussion. So long as the vitality of our museums is kept up by the constant supply, year after year, of thousands of new butterflies and other insects imported from the tropics, so long as they can interest the public by the fact that so many new fishes or birds, bats or snakes, are described in them, so long, naturally, travelling naturalists will pay little heed to the search for those inconspicuous animals which are

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alone of any importance to the question here under discussion. I myself, having been one of those very travellers, must own myself guilty of such an oversight; but if I nevertheless may venture here to avail myself of the few incidental observations I have made, they allow me to come to the following conclusion, the same that we are led to by Schmarda's observations—that, in fact, in by far the greater number of the Infusoria, Rotatoria, Tardigrades, fresh-water Crustacea, and Worms, the European and American species are so extremely alike that they seem in many cases to be perhaps even specifically identical. If they were suddenly transferred to Europe, they would scarcely alter the character of the fauna of our lakes and rivers in any degree.

I say *scarcely*, intentionally and with due consideration; for a few exceptions, at present unfortunately too little known,

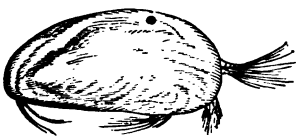

FIG. 80.—*Cypris* sp., from the Philippines.

seriously disturb this uniformity; or else forms are entirely wanting in other countries which, so far as our present experience goes, belong to the characteristic fauna of the fresh waters of Europe. To this latter category belong the crustacea included in the group of Phyllopoda, which, wherever they occur, live almost, or quite, exclusively in pools or sloughs. *Apus* (see fig. 33) and *Branchipus* are the most familiar of the European forms of this family. Quite similar species occur in North America, Australia, the Feejee Islands, and Africa; but for seven years I vainly endeavoured to discover any species whatever of this group in the Philippines; they are equally absent from the Pelew islands, and it would seem that they do not occur in the Malayan Archipelago. But the Daphnidæ and Cypridæ, which are associated with them in Europe and America, are nowhere wanting. I have found them wherever I have sought for them; nay, indeed, species which were deceptively

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like our own. Thus the question arises as to the cause of this absence of Phyllopoda in countries where other forms can exist which live under the same conditions, since both belong to the animal group whose distribution on the globe seems to be caused essentially by the action of winds. We know that all these forms produce eggs which can be dried without losing their power of development, and that many actually require to have been dried before the young can develope and escape. These eggs too are minute and light, and certainly can be borne as dust before the wind. Why then are Apus and Branchipus absent in tropical localities where the other crustacea nevertheless occur? This striking anomaly is, however, as is easily shown, more apparent than real. The establishment of such forms depends not merely on the practicability of their germs being universally distributed in the manner above indicated, but also on the favourable accessories in the new conditions in which they find themselves. Hence it would be very possible that the eggs of Apus and Branchipus might reach the same tropical lands as those of the other crustacea, but not find there the circumstances that would favour their development. What the hindering causes may be it is difficult to say, for we are now only at the very threshold of our knowledge of the vital conditions of these creatures; but if it were allowable to generalise from Brauer's elegant experiments we might say that perhaps it is the absence of winter-cold between the tropics which constitutes this hindrance, for he has shown that the eggs of several Phyllopoda, at any rate, develope most rapidly, or perhaps only, when they have previously been exposed to a very low temperature, nearly down to the freezing point.

The very general uniformity of the lower forms of fresh water animals is, in the second place, interrupted by the occurrence, among numerous species of typical European character, of isolated forms which appear perfectly foreign among their associates. Thus, among many Rotatoria in the Philippines which can hardly be specifically distinguished from the European species, there are a few quite divergent forms. The most remarkable of these is one named by me *Trochosphæra æquatorialis* (see fig. 81) and which I described as long ago as 1872.

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I found this genus exclusively in Mindanao. What is the reason that it is absent from Luzon and Bohol, where the same external conditions of existence would seem to prevail as on the southern island? It is impossible to suppose that the eggs have not been able to find their way thither; but what the numerous causes may be which affect their development, in one place favouring and in another preventing it, is not at present known.

A second example of the same kind is offered by the forms of *Branchipus*. Species of this genus live both in Europe and America. The species occurring in the two continents, though easy to distinguish, still are so similar that the American species might be transferred to Europe and *vice versâ* without changing anything in the character of the fauna of either country. But, associated with them, live a few other very divergent forms, particularly the very singular *Thamnocephalus*, which

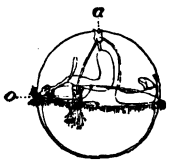

FIG. 81.—*Trochosphæra equatorialis*, a Philippine species (Rotatoria).

disturbs the uniformity of the American Branchipoda by its occurrence in the south of the Union. Here also the causes are perfectly unknown which prevent this genus from developing fully in the higher latitudes of North America; but we are obliged to assume that there are such hindrances, since it is difficult otherwise to see why they should not develope in the north just as well as the eggs of the other Branchipoda which are distributed with great uniformity over the whole continent, and which everywhere develope in the same manner. It appears to me that Brauer's researches—so often alluded to—if not as yet fully available, contain the germ of future and more fertile inquiry in this direction, and it is only to be wished that Brauer may not long remain in sole possession of this field, for a combination of forces will in this, as in every case, lead sooner and more certainly to the desired result.

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2. Currents and winds as limiting the distribution of species.—When we reflect on the mode in which alone winds and currents can possibly convey animals from place to place, it becomes self-evident that they must very frequently act also as hindrances to the distribution of species. Ships, drifting ice with the boulders, erratic blocks or drift-wood transported by it, trees uprooted from the land, and the leaves and dust often carried to great distances by storms—all these serve from time to time and with more or less frequency for the transport of many kinds of animals. And since storms, winds, and currents, in spite of many variations in their courses, are still on the whole very constant, it necessarily follows that those animals which either do not come within their range, or which cannot bear transmission by such means, are excluded from distribution by these agents. Elephants could never be conveyed to any distance on floating trees, as small snails can, or even such mammals as live among their branches; wingless land birds, like those of New Zealand and Madagascar, are incapable of migrating to any distance; but still, in these and all similar cases, currents serve as a means of separation only because the nature of the animals concerned forbids their availing themselves of them. Thus the action of winds and currents is dependent on that of the animals or co-operates with it. Even in cases where the currents appear to act quite independently, their influence is always dependent on other conditions which may be associated with them. Thus, for instance, many animals are extremely susceptible to variations of temperature; consequently, if any warm-water animals are borne by a current from the region of warm seas into a cold one, they must in all probability perish very soon. Here, then, the currents might have acted as promoting and aiding distribution, but this result was completely neutralised by the contemporaneous action of a diminution of warmth. In the same way very often some animal may be carried by the wind from one island to another without any favourable issue; for its establishment in the new locality depends, as we know, not merely on its safe arrival there, but also on the creature's finding in its new home

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all the other conditions of life favourable for its living and reproducing its kind.

Currents themselves must no less have a dividing action in some cases. It is well known that all floating objects, such as drift-wood, leaves, trees, &c., gradually drift to the edge of the stream, even though they may have fallen into the middle of it. Every navigator is familiar with the phenomena resulting from this, and knows that the western and eastern limits of the Gulf-stream are both indicated by a broad band of accumulated sea-weed, wood, leaves, and other objects. This tendency of the current to clear itself—or clean itself—is stronger in proportion to its rapidity and strength. Hence, objects torn by a stream flowing between two islands from the one lying to the left of it, could be borne to that on the right side only under specially favouring circumstances; and *vice versâ*, those brought from the right could never, or very rarely, be carried to the opposite side. Thus a mixture of the faunas of the two islands might be hindered, or at any rate rendered extremely difficult, simply by the action of the current flowing between them. Only those free-swimming animals which might be able to overcome the mechanical resistance of the current to which they would be exposed in their attempt to cross it, would be in a position to escape its influence. That this action of the current is theoretically inevitable cannot be disputed; still, the question may of course be raised as to whether actually it often comes into play.

Certain phenomena attending the distribution or migration of animals do in fact leave no room for doubt that this dividing action may often be detected, above all in marine currents. We have already met with a few examples in previous sections. When we were considering the striking circumstance that the islands lying close to Africa have a quite different fauna from that of the neighbouring continent, we mentioned this as a factor; for that fact was intelligible only on these grounds, and we pointed out, on the one hand, that the stream flowing from Europe, on the north, was, from the course it takes, able to introduce a quantity of European forms into these islands, while, on the other, any species of animals carried off from the African

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shore must be deprived of every chance of reaching these islands, since a dividing current flowed between them. I have further remarked above, how sharp a contrast is defined between the marine fauna east and west of the meridian of the Cape of Good Hope; to the east, the animals of the Indian Ocean brought down by the Mozambique current, and a multitude of beautiful forms are abundant; to the west, there is the greatest poverty of animal life and a quite different set of species. No mixture of the two occurs, as it would seem; and this is confirmed by the statement—never, so far as I know, contradicted—that the whale of the Atlantic never crosses the meridian of the Cape, although it is certainly one of the strongest swimmers of the deep. I have before shown how difficult it must be for the larger land molluscs to cross arms of the sea, and this is visible even on a small scale. To the north of Luzon lies a small group of islands known as the Babuyanes. Their land-snails belong on the whole to the groups typical of the Philippines; true *Cochlostylæ* for the most part, but quite different on the eastern and western islands. Species occur on the latter which bear a remarkable resemblance to those of the west coast of Luzon or are quite identical, while on the former only such are found as are especially characteristic of the eastern side of that island. This may in part result from the fact that the vegetation of the eastern and western Babuyanes seems to be tolerably dissimilar, but this would not remove the influence of the currents flowing from the east and west of Luzon—an influence which is plainly discernible—it would only make it indirect. For on Luzon, too, the same difference is perceptible in the vegetation of the eastern and western portions; in the east, forests without limit; in the west, cultivated land and pasture. It would be easy to cite a great number of similar cases in which the dividing action of marine currents would be more or less discernible, but it must suffice here to discuss in detail another of the more interesting examples.

The difference between the fauna of the islands of the Malayan province and that of New Guinea and New Holland long since attracted the attention of naturalists. Schmarda defined the Australian region as in direct contrast to the Indian.

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Certainly he includes in the Indian the Sunda islands, which Wallace, who first attempted to explain this contrast, placed in the Australian region. The limit-line, which, according to Wallace, sharply divides these two regions, runs between the two islands of Bali and Lombok, close as these two lie to each other. He reckons the fauna of Bali with that of Java, while that of Lombok is said to be completely different, and to belong to the Moluccas. From thence the limit between these two provinces runs somewhat to the north-east, between Borneo, which still belongs to the Indian, and Celebes; it then turns abruptly to the east; thus all the Philippine islands are thrown into the Indian region, while a few of the smaller groups, forming a connection between Mindanao and Gilolo and New Guinea, lie south of this limit-line and are thus included in the great Australian region. The line thus laid down has been designated as Wallace's line, in honour of its founder.

It cannot be disputed that this line seems, in fact, a very natural one, if only the birds and mammalia are taken into consideration and the insects not brought into the comparison. In the Australian region the Marsupials, birds of Paradise, Monotremata, lyre-birds, cockatoos, cassowaries, and the very peculiar Trichoglossidæ; in the Indian region, on the other hand, the apes, lemurs and flying squirrels, *Galeopithecus*, and many other Mammalia which are absent from the Australian region. Among birds, the Argus pheasant, the peacock and *Euplocamus*, the various pigeons, and of parrots the *Loriculus* and *Palæornis*, with many others, never occur in the Australian region. We must not, however, leave out of the question the fact that many of these forms, or of others equally characteristic, not rarely pass across into the neighbouring region, where the two come into contact. Wallace himself points this out. But the contrast is much less sharply defined in the Reptiles, Amphibia, and even the Insects; thus Pascoe, who has the most perfect knowledge of the Coleoptera of the eastern hemisphere, says that, as regards its beetles, New Guinea most positively belongs to the Indian region, and that they are quite clearly distinct from the Coleoptera of New Holland. Hence the contrast indicated is not absolute throughout, and Wallace himself, in his

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book on the geographical distribution of animals, repeatedly points out that many species encroach on the limits of the neighbouring province in a very singular and incomprehensible manner; and he justly infers that there must be some peculiar means of dispersal as yet unknown to us, by which these species are enabled to overstep the limits apparently assigned to them by nature. Moreover, he speaks of the fauna of the island of Celebes, included in the Australian region, as exhibiting so remarkable a mixture of animal types that it might just as well be included in the Indian region. But irrespective of these forms, which prove that Wallace's line does not indicate an impassable frontier, there yet remains so vast a number of extremely different species, peculiar to each of these regions and belonging exclusively to one, that the sharp distinction so long recognised between them appears fully justified.

The question now is whether this distinctive contrast can be explained, and more particularly how it happens that two islands lying so close to each other as Bali and Lombok should by Wallace's line be placed in two different regions of animal distribution. Wallace himself—who, so far as I know, was the first to attempt to explain this phenomenon—does so as follows :—

He assumes that at some former period the Indian continent and the Indian islands as far as Java, Borneo, and the Philippines, were connected; and that, in the same way, Australia with New Guinea, the Moluccas, and Celebes, were in connection, and that only the group of islands from Timor as far as Lombok were perhaps excluded. This last must probably have been divided from Java by a deep sea; and it was not till a later period that Bali by the side of Java and, the smaller islands as far as Lombok by the side of Timor, were raised from the bed of the sea. The differences of the fauna which nevertheless occur on the individual islands of each region he endeavours to account for by their separation at different periods from the Indian or Australian continents.

Now, it certainly cannot be disputed that very many circumstances in the distribution of the land animals on these islands argue in favour of this view; thus, for instance, the fact, un-

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known to Wallace but discovered by myself, that at a former period an elephant[117] was found on Mindanao, the most southerly of the Philippines, can scarcely be explained except by the supposition that a direct connection existed between this island and the Indian continent, or an indirect one by a junction with the larger Malayan islands. For any transportation of this species, which is very nearly allied to the dwarf variety of Indian elephant, by a passage across the sea is not to be thought of. Nevertheless, I believe that this hypothetical connection of the islands and mainland is not sufficient by itself to explain even those facts that are already known to us as to the distribution of Indian and Australian forms on the islands lying between the two continents. Even Wallace himself falls back on a number of other causes, and in order not to abandon his general principle he suggests a hypothetical history of upheavals and subsidences, so numerous and various in the different islands that, in the total absence of all geological proof of them, we feel ourselves gradually withdrawn from the *terra firma* of justifiable speculation and floating in the clouds. It seems to me that there is a very general predilection for too readily constructing sunken continents. Whenever any extensive resemblance between the faunas of two distant countries is discovered, or even imagined, a bridge of mainland is always freely brought in as the only mode of accounting for this resemblance. No doubt it is the most convenient of instruments, and all the more easy to work with, *i.e.* to use as evidence for a theory, because it is absolutely impossible to prove the fallacy of the hypothesis by the method of observation, the only way open to the naturalist.

But until the question is finally settled whether two parallel series of animal development might not have proceeded independently in two countries remote from each other, we can never venture to regard the resemblance of two faunas as conclusive evidence of their primæval actual connection; nay, it even seems to me that the two historical series of species of the horse, recently discovered both in Europe and America, may on the contrary be regarded almost as a proof that each series was developed independently in the two continents and yet led to

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the same result: namely, the production of the horse. However, I leave this an open question; thus much only I think may be insisted on: that in such speculations this possibility should never be lost sight of, and, at the same time, that all the different causes which may have had a share in influencing the distribution of animals must be fairly investigated and weighed before it is possible to set up any one special method of explanation as the only correct one to the exclusion of all others.

At any rate it is perfectly certain that winds and marine currents sometimes promote and sometimes hinder the diffusion of species, both directly and indirectly. One species may be able to cross a pretty strong current at a sharp angle, while another may be prevented by a feeble wind or current from reaching an island lying very near; certain kinds of seeds can only be transported by the wind, others again only by the sea; where, on an island or a group, some particular plant is absent because its seeds could not reach it, there of course the animals also will be absent which depend on it for food and are monophagous. The relations thus occasioned between the faunas of islands in two contiguous regions, such as the Indian and Australian, are of course extraordinarily various, complicated and difficult to investigate; but this does not justify us in neglecting them. It may be more convenient to argue from upheavals and subsidences which may be imagined in any required number, or from hypothetical intervening continents whose former existence can be neither proved nor disproved; but the easiest method is certainly not always the most accurate—I may almost assert that it hardly ever is. But in this particular case it does not appear to me to be so exceptionally difficult to detect the relative conditions if we do not wilfully shut our eyes to them.

If we now reflect more particularly on what has been said here and in a former chapter as to the mode of action of currents, the view is irresistibly forced upon us that it is possible that the differences here pointed out in the distribution of animals may, without exception, be explained by their agency without assuming any former material connection between the islands and the nearest continents. Granting that the larger number of the Malayan islands and of those in the vicinity of

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New Guinea did not rise from the sea until quite recent times, still the colonising of the islands from the neighbouring continents might have taken place in such a way as to involve a distribution such as is actually presented to us there. All the larger Mammalia, being incapable of overcoming the strong currents prevalent there, would have been excluded from immigration into the newly formed islands; only the smaller species, that cling to trees, could have been carried across seas by those currents; and it agrees with this that we find all the Marsupials out of Australia, as in New Guinea, the Moluccas, and Celebes, belonging exclusively to the climbing genera. And that these should not have succeeded in crossing Wallace's limit-line is the inevitable and very intelligible result of the tendency of currents to 'clean themselves,' as before described. This tendency results from the circumstance that such a current is always a little higher in the middle than at the sides. Hence objects floated off by the right margin of a current flowing through the straits of Timor or Celebes, or between Bali and Lombok, could reach the left shore only under some specially favourable circumstances; they would usually remain on the same side, particularly when they were passively borne along, as would be the case with uprooted trees and so forth. In looking at a map on which the currents in question are laid down, it is at once seen that the currents flowing from Australia and the southern part of New Guinea are suddenly diverted from their slightly westerly or quite northerly direction to a north-easterly or quite easterly flow, exactly by the very island —namely Celebes—where the mixture of Indian and Australian forms is most conspicuous. Land animals—such as land-snails—of which the transportation can only be effected by currents must have been subject to the same influence, and it is therefore quite intelligible when we find that two islands lying so close together as Bali and Lombok exhibit less similarity than, for instance, Celebes and Java; for the current that parts those two little islands is so strong that it must be quite impossible for molluscs, or other creatures that avail themselves of drifting trees for their voyages, ever to pass from one island to the other. On the contrary they might, under certain circum-

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stances, easily cross the boundary originally set to their passage by the current on the longer voyage to Celebes; very easily, indeed, when, by slight variations in the strength or direction of the monsoons and in the surface currents caused by them, a temporary change was produced in the direction of the normal current flowing between Celebes and Borneo—known as Wallace's current—which is merged in the return current of the Pacific Ocean. All those animals, on the other hand, which might have other means of transport at their command, would be rendered independent of the agency of this current, whether in separating or in mingling the faunas; but of course only so far as they were not monophagous, and thus absolutely dependent for food on certain plants of which, again, the extension of range was subject to the action of the said current. In pursuance of this mode of viewing the matter we should then have to inquire whether those insects and birds which appear to have migrated from the Indian region to the Australian, and *vice versâ*, may not be polyphagous and easily satisfied with various kinds of food; and, on the other hand, whether, as an inevitable corollary, those forms which are confined to particular islands or districts may not be monophagous or dependent on certain forms of food whose extension of range from one island or region to another is prevented by the agencies under consideration.

This, however, is not the place for pursuing this inquiry in detail, nor do we as yet possess sufficient materials for it in the form of well-confirmed observations. But so long as the general observations we do possess allow of no positive conclusions, we are, on the other hand, not justified in rejecting any possibility as erroneous, and consequently Wallace's hypothesis must for the present remain open to discussion; the arguments here laid down in opposition to it are so too, in the same degree and for the same reason, and it must be left to the future to decide between them. Still, I am of opinion that the hypothesis I have put forward may claim the advantage of appealing for proof only to such elements as can be brought under direct observation, while Wallace's is intrinsically incapable of demonstration by observation.

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It follows from all this—as it seems to me—that the action of marine currents, as means of separation and amalgamation in the distribution of organic life, must be made to bear a larger part than it has hitherto done, in inquiries as to the origin of the present fauna of the globe from those of former periods. For if we conceive of this course of development as a mechanical process and make it our purpose to trace those determining causes which have been merely mechanically operative, this can never be done by propounding a more or less plausible hypothesis, but only by methodical investigation; nay, only by the method of modern physiology—as much by a due reference to all the factors together which must be taken into consideration, as by successively identifying the influence which each of them, separately, may or must have had.

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CHAPTER X.

A FEW REMARKS AS TO THE INFLUENCE OF OTHER CONDITIONS OF EXISTENCE.

BESIDES those external conditions of animal life which I have treated of in the foregoing chapters, there are others of which the effects in certain cases may be of much greater consequence; which may indeed not unfrequently neutralise the effects of apparently more important ones, while they may nevertheless at present escape any close investigation. Such, for instance, are the effects of gravitation or pressure, of electricity, of the aggregate condition of the surrounding medium, and many others. They are often apparently insignificant as compared with temperature, light, nutriment, &c., not because they are of themselves unimportant, but only because we know much less of their normal effects on the life and growth of animals than of the conditions we have hitherto been discussing. Their action almost entirely eludes those methods of research that I have hitherto employed and which alone I acknowledge as the right ones; consequently in the following brief discussion of these points I find myself wholly thrown back on hypothetical interpretations of such observations as have been incidentally made. Nay, the number of these observations is in itself so small, that in many cases they do not even suffice as a basis for such an hypothesis; and finally it must be acknowledged that sometimes the interpretation hitherto offered of certain facts has been founded on gross errors which, however, are widely diffused and, as it would seem, almost ineradicable.

The effects of gravitation and pressure.—The selective influence of gravitation and its bearings on the organisation of

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animals are in many cases very conspicuous and intelligible. Thus, for instance, it is perfectly evident, and has long been acknowledged, that by it a certain standard is fixed for the bulk of the animal's body which cannot be exceeded without endangering the life of the individual. If, for instance, we grant that the structure and specific gravity of any animal are factors bearing a relation to each other that does not allow of any considerable variation, and also admit the possibility of its growing beyond the normal standard of size, the animal would finally be so large that it could not move its own weight, since its gravity must increase in geometrical progression. Of course the maximum of height or length attainable by particular animals varies with their organisation, and hence must differ in different groups of animals. Birds are the most remarkable in this particular; in them the standard of bulk generally attainable would be remarkably small with a specific gravity the same as that of mammals, and their life in the air. But there are in their organisation certain adaptations which make the maximum bulk they actually attain tolerably high; these are the pneumatic bones and the air-cavities between the muscles and in the body, which are sometimes extensively developed, particularly in the strongest flyers, as for instance the Albatross. By these the bird is enabled to attain a volume of which the weight could not long be carried by the most powerful flyer if it corresponded to that which any quadruped of the same size would have to move. A very interesting illustration of this peculiarity is afforded by one of Professor Marsh's latest discoveries in America. The wonderfully rich deposits of fossil remains in the Rocky Mountains have yielded to his search a Reptile which, according to careful estimates, from a restoration of its hind limbs, must have attained a height of at least eighty feet.

According to the calculation made by a mathematician—a friend of Professor Marsh's—this creature would in that case actually have exceeded the maximum size it could have controlled, under the supposition that in general organisation, and therefore in the specific gravity of its body and bones, it exhibited no deviation from that of the largest reptiles now

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living, the crocodiles. But in point of fact the specific gravity of its bones was less, for they are traversed by very large cavities which, Professor Marsh says, have all the appearance of having been air-cavities, and after careful investigation he does not hesitate to pronounce them decidedly to be such. I, in company with him, examined these bones, though not, I must admit, at any great length, and I confess that from their structure alone it did not seem to me possible to prove that this reptile had actually had pneumatic bones like those of birds. It is, however, possible that the calculation, which must have been intrinsically one of great difficulty, may have been erroneous, and in that case, in my opinion, the most weighty argument for Professor Marsh's view would disappear. But if in fact his friend's calculation as to the maximum size of a reptile having the specific gravity of the crocodile is correct, I believe also that the large cavities which undoubtedly exist in the bones of that fossil creature can have been nothing else than air-cavities, whose function it was to render the animal light enough for it to carry the still considerable weight inseparable from such an enormous mass.

The media in which animals live also exert a certain pressure depending on their mass and specific gravity, and it is easy therefore to imagine that all creatures which either fly in the air, swim in water, or creep in mud, must be affected by the pressure of the superincumbent mass. This, of itself, is quite true; but this true view has, even in quite recent times, often led to perfectly false issues. The most striking instance of this perverted application of a true idea is offered in the case of animals living at great depths, in fresh as well as in salt water. It used formerly to be said, and the idea is not uncommonly expressed even at the present day, that it was most wonderful that animals generally, and more particularly such delicate structures as Polypes, many Worms, Univalves, &c., were capable of enduring the enormous pressure of the vast volume of water above them, amounting in ocean depths to that of many atmospheres. But, put in this form, the idea is simply absurd; for the soft-bodied creatures living at the bottom of the sea are no more conscious of the pressure above them of a

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column of water, theoretically estimated as that of many atmospheres, than we human beings, in the normal condition of our bodies, are aware of the weight above us of one atmosphere; and simply for this reason, because the pressure is equal on all sides, and because they are themselves permeated by fluids which, as is well known, are almost incapable of compression. The weight of a high column of water can never affect an animal at the bottom, excepting when the animal has cavities in its body which are filled either with a fluid of less density than the water, or with gases. In the latter case particularly, the effects are, as is well known, easy to observe, since gases are in a high degree compressible. Divers who plunge into great depths—as, for instance, the pearl-divers in the Indian seas—or, on the other hand, people who climb mountains to a great height, often suffer severely from the difference of pressure in the external atmosphere and the tension of the air in their lungs, or the pressure in the internal vessels: the divers because the increased pressure causes compression of the air in the lungs; the climbers because, on the contrary, the heavier air in the lungs tends to expand under the reduced atmospheric pressure at a great height. When a man has accustomed himself to the lighter atmosphere of high mountains—*i.e.* to the smaller pressure—he frequently finds it more healthy and agreeable than that of the plain, or at least equally so. Birds, which often come down to the plain from the giddiest heights with extreme rapidity, must evidently be capable of accommodating themselves much more promptly than man to the alteration of pressure, since not their lungs merely but their pneumatic bones and all the other air-cavities of the body are filled with air.

On the other hand, there are animals which have cavities filled with gases in their body, but which are not capable of effecting a change from the compression which must be the condition of such gases at considerable depths, so rapidly as birds nor even as man; not so rapidly indeed as quick alternations in the external pressure would require. This is the case with fishes provided with a swimming-bladder. An interesting instance is afforded by the little fish of the Lake of Constance known as the Kilch. These fish, allied to the Trout family,

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are a favourite article of food. They are caught in nets and brought to the surface of the water; they come up invariably with the belly much distended; the air in the swimming-bladder, being relieved from the pressure of the column of water, has expanded greatly and occasioned this unnatural distension, which renders the fish quite incapable of swimming. Under these conditions the fish is naturally unable to live for any length of time. But the fishermen of the lake have a very simple remedy; they prick into the air-bladder with a fine needle; the air escapes with some force, the distension subsides, and the fishes are enabled to live under totally changed conditions as to pressure, even in quite shallow water and at the surface, swimming quite as freely as their companions, the

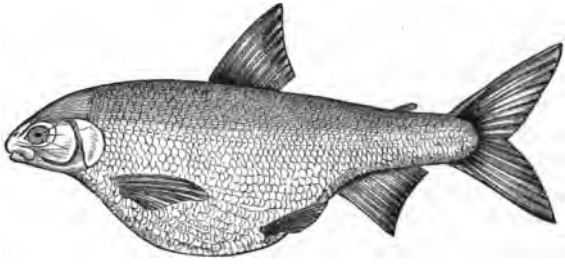

FIG. 82.—The Kilch of the Lake of Constance (*Coregonus hiemalis*), showing the distension caused by the expansion of the air in the swimming-bladder.

natives of the surface water. Hence the Kilch is confined to a certain depth, because it is not capable of accommodating the tension of its swimming-bladder to the change of pressure in the column of superincumbent water. Since, moreover, in the Kilch the pressure from within outwards is the same as the external pressure, or must at any rate be very nearly the same, the mechanical problem stated above has no existence for this fish, nor for any other creatures living under the same conditions. It can arise, in fact, only in those uncommon cases—such as would seem to be offered, for instance, by the whale—where an animal furnished with internal air-cavities plunges from the surface of the sea down to considerable depths and remains there for some length of time; in these it is evident that some

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contrivances must exist which neutralise the ill effects of the compression of the contained air—which must undoubtedly take place.

In the instances here adduced, and in other similar ones, of the action of gravitation on animals, the effects are obviously merely selective; all the individuals which are not qualified to accommodate themselves to the actual conditions of pressure must perish or seek a more suitable habitat. But gravitation may perhaps have also a direct determining action, perhaps in a mode analogous to that by which the growth of the roots of plants, or the structure of the underside of leaves, and other things may directly depend on gravitation. The theoretical possibility of this influence is beyond dispute; but we know very little of its actual effects and extent. Nor can there be any doubt that animals, in consequence of their greater freedom of movement, are in a great degree independent of it; and any extensive influence of this kind, such as is undoubtedly manifested in plants, must be out of the question, except as regards sedentary animals, such as corals, sponges, bryozoa, &c. How far, in such creatures as these, gravitation may have an effect in determining the general form of the colony, or of the individual animals and their organs, is perfectly unknown, and it is difficult to see by what means it would be possible to ascertain experimentally the effects of gravity upon such animals. For all those contrivances which have been successfully employed on plants, to allow gravitation to exert a perfectly independent influence on their growth, cannot be applied to animals, and, so far as can be seen, we can only fall back on the interpretation of those experiments which Nature herself performs on growing animals under the normal conditions of their existence. It is evident that we can thus only arrive at more or less bold or plausible hypotheses; for the fact cannot be too often insisted on that experiment alone can ever enable us to explain the causes lying at the root of any particular phenomenon in the development of an animal. All theories deduced only from the visible phenomena without the counter-check of experiment are mere clever suggestions, which only serve to conceal our ignorance, and in fact hinder any advance. Thus, for instance,

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it has been asserted that gravitation has an influence in determining the direction of the growth of the embryo in Mammalia. But it seems to have been forgotten that in most cases of viviparous animals the position of the embryo in the uterus is by no means constant, but alters in many ways during its development. If, in fact, gravitation were here of so much importance as has frequently been assumed, scarcely any normally developed animals would be born; for we know, from the remarkably complete experiments of Marcel de Serres, that such embryos as normally assume a position of equilibrium for their development in the ovum—as, for instance, those of birds—are invariably deformed in the most irregular manner, if they are constantly moved into other positions and so the original equilibrium is disturbed. In the ova of many invertebrate creatures the developing embryo floats in a surrounding fluid; so that under any inversion of the whole ovary or cluster of eggs all the embryos recover the same position, since the centre of gravity, lying out of the centre of the body, always sinks to the bottom. In such cases as these gravitation evidently acts to prevent any disturbance of the equilibrium; but it is very questionable whether at the same time any effect is thus produced on the process of development of the embryo itself within the egg. That the limbs—as our arms and legs—are subject to the conditions of gravitation allows of no doubt, and its effects may very possibly tell on the same parts of the body in the developing embryo while still in the uterus. But how far this influence, which, no doubt, actually exists, may contribute to determine the normal formation of animals and their organs, is perfectly unknown, and cannot be ascertained by any merely theoretical discussion.

Darwin adduces many instances which prove that even the bones of the skull may be modified by gravity, or by pressure in whatever manner exerted. Burns and repeated convulsions in certain muscles have been known to affect the form of the bones of the face; the same effects have been produced when human beings during youth have been forced to keep the head constantly in a fixed position; it is supposed that in certain persons—for instance in shoemakers—who are obliged to keep

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their head bent down for many hours together, the forehead acquires a prominent development of the frontal bones. Darwin has shown, moreover, that the forward lop of one ear of the long-eared rabbit induces a corresponding forward growth of almost every bone of the skull on the same side, so that it is perfectly asymmetrical. Nay, even the growing brain appears to exercise a decided influence by the pressure it exerts on the shape of the surrounding bones. But in all these, and many other cases which might be enumerated, the only fact ascertained with any certainty is that the growing parts themselves, as well as other organs connected with them, may be modified by pressure and by their own weight; no determined standard for estimating this influence is in any instance fixed, and we learn from them absolutely nothing as to how far this influence may be efficient in determining the production of the normal types in animals now living. So far as I know, as yet only a few attempts have been made to refer the normal form of the skulls of vertebrate animals to the effects of such constant pressure; the most important of these are certainly those of Lucae in his researches as to the skulls of mammalia, and those of Gudden in his investigations as to the growth of the skull of the rabbit. Lucae, however, altogether disregards any experimental treatment of the question; and what we learn from Gudden, valuable as it may be to physicians, physiologists, and anthropologists, is of no present value as affording any methodical standard for our inquiry.

The influence of solid bodies.—The aggregate condition of solid bodies must decidedly have a certain influence on the animals whose life is passed in digging or boring into them. The highly sensitive nose of the mole, for instance, must certainly exhibit a quite different structure from that of the prairie-dog, or Dipus, which uses it, as I myself have seen in tame individuals, to beat the earth down firmly in its dwelling. The various and extremely dissimilar structures which occur as organs for burrowing in both vertebrate and invertebrate animals, are so perfect in their adaptation to their function that from the structure of the legs, which are the limbs most commonly employed for this purpose, it is easy to infer the mode of

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using them; nay, the whole form of the body may be thus determined, as in the turnspit, a dog with a propensity for digging, or in the cylindrical form of the boring beetles of the genus *Bostrychus*. It is clear that these adaptations of the organisation of certain animals to the resistance offered by the conditions under which they live must be a powerful means of selection by which all the individuals which are not strong enough to overcome the obstacles opposed to them must be eliminated. And since any variation in the aggregate conditions of the soil, wood, or stone, in which such creatures live, must be either very insignificant or perhaps wholly absent, the point of 'stable equilibrium' must soon be reached between the strength of the digging organs on one side and that of the obstacle to be overcome on the other; the variations which easily may occur in other surrounding conditions—as in the temperature, moisture of the atmosphere, salt constituents of the water, nutriment, &c.—can in such cases but very rarely be efficient causes in effecting any modification in animals exposed to the former influence. Nevertheless, such modifications of the organs of many animals as were dependent on the aggregate conditions of solid bodies must have occurred in the course of their phyletic or generic development; for, if we are to suppose that boring or burrowing animals descended originally from such as did not bore or burrow, in the process of modifying the organs adapted for motion above ground into such as were fitted for subterranean progress, organs which were originally destined and contrived for walking, running, or swimming, must have abandoned these functions to assume new ones, and thus have been so far modified in structure that they could be used in the best way for the purpose. But we know nothing as to how such alterations in the habits of certain animals—urged by some inward prompting—may have been able to occasion these modifications in the structural characters of the organs in question. It is well known that a determined mode of motion, or on the other hand the strength of the obstacle to be conquered, may have a certain effect on the strength of the muscles called into play, and, through them, on the power of resistance in the fulcrum joints of the bones, and ultimately on the

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structure of the skeleton. But between a merely mechanical modification of a bone during the lifetime of an individual and the differentiation which the leg of some primæval mammal must have undergone before it could have given rise to such a strikingly peculiar limb as the foot of the mole, there lies a great gulf which no experience hitherto attainable enables us to bridge over. The most we can say is this: That, beyond a doubt, some cause unknown to us must exist—or must have

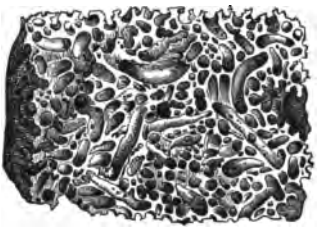

FIG. 83.—A piece of wood bored by *Limnoria terebrans*, from Heligoland.

existed—in the nature of different animals, which has occasioned them sometimes to abandon their original habits or to alter them.

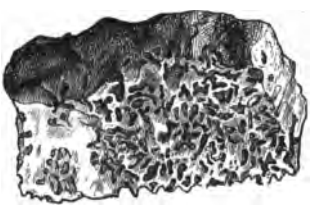

FIG. 84.—A piece of solid limestone bored by *Limnoria terebrans*, from Ireland.

The two woodcuts here given illustrate a very striking case in point. It has long been known that a small Crustacean, *Limnoria terebrans*, attacks the hardest kinds of wood—like the well-known ship-worm, *Teredo navalis*—and pierces it in all directions with its cylindrical galleries (see fig. 83). But it is perhaps less well known that the same species attacks solid limestone in the same manner. The stone of which the annexed cut shows a small portion (see fig. 84) I myself picked up

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in Ireland, one of thousands, both larger and smaller, which were pierced in the same way by myriads of these small boring animals. Unfortunately it was impossible to examine the animal very minutely at the time, and I could only ascertain that it certainly was the *Limnoria*, so familiar to me on the shores of Heligoland and elsewhere, which in Ireland had not disdained the hardest limestone. Very likely closer investigation might reveal certain differences in the different individuals of the same species boring in wood and in stone, as to the structure of the organs used in boring, and which might show an evident relation between those organs and the hardness of the substance bored into. It is known, too, that certain species of sea-urchin sometimes bore into very hard rocks, while in other places they do not. In other instances the form of the animal shows the direct effects of contact with solid bodies; this is the case with many sedentary animals or those enclosed in a solid shell. Many oysters, and such shell-fish as establish themselves on rocks or wood or in fissures, frequently adapt their shells very exactly to their position, and the form thus given to them might easily become constant, and even a fixed specific character, if a similar position were adopted by all the individuals of the species. But here again, we do not know how far the determining influence of the solid object, which in some measure moulds the shell, may extend, for no experiments exist which can conclusively prove that in such cases the moulding power of the position has been exclusively effective with no assistance from inheritance, and we therefore are not in a position to assert that this explanation of the observed cases, though in itself extremely plausible, is in every respect the right one. In order to verify this usual and apparently correct interpretation of these forms of shells, it would be necessary to prove by experiment that species which had hitherto lived in some particular situation lost the form thus impressed on their shells as soon as their young were compelled to establish themselves in a position different in character; and, yet more, that they could be made regularly to assume quite different shapes according to the differences in their new habitat. Experiments of this kind that have been made with oysters undoubtedly prove that a certain

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and somewhat extensive influence is exerted upon them by the conditions of their position. Nevertheless, they yield no satisfactory conclusion as to the amount of these mechanical effects, though their existence cannot be disputed.

And we are still worse off with regard to other influences, which certainly exist, although they remain up to the present time perfectly unintelligible to us. Thus it can hardly be doubted that the electric tension of the atmosphere or of terrestrial magnetism must have some effect on animals, and attempts have not been wanting to refer certain phenomena of animal life to these causes. Thus, for instance, at one time the view was put forward that migratory birds directed their flight towards the magnetic poles in the Old and New World; an opinion which certainly seems to have been based on the tempting but usually misleading principle of *Post hoc, ergo propter hoc.* We may, however, congratulate ourselves that the latest and most thorough work on the migration of birds—that of Palmèn—sets aside this mysterious power of the magnetic poles as purely fabulous. Even with regard to the effects of atmospheric electricity, we may surmise their existence, but cannot grasp it, and remain unable to come to any decision; that the discharge of electricity in the form of lightning can occasion death is all that is certain. But this, of course, is of no great importance, as it never can be a factor in the origination of a new species or the extirpation of an old one; with regard to such results as these, only the feeble electric tension of the atmosphere need be taken into consideration—and this probably is not even perceptible to most animals—since that alone is capable of exerting any constant influence. Lately, and particularly in France, naturalists have begun to investigate the effects of electric currents on animals and on their development, and have already arrived at very remarkable results. Thus, Onimus found that the ova of frogs developed more rapidly at the negative pole of a constant current than at the positive pole; Wagner supposes that he has observed an effect of electricity in altering the colours and the form of the wings of butterflies. These and the observations of Pigeon, Chauveau, and others do not, however, at present, allow of our applying them to

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the question of immediate interest to us here; for our purpose it must first be proved, or at any rate shown to be probable, that electricity generally may exert a determining and ascertainable influence on the normal growth of animals, and this has not been done by any experiments hitherto made.

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SECTION III.

THE INFLUENCE OF LIVING SURROUNDINGS.

CHAPTER XI.

THE TRANSFORMING INFLUENCE OF LIVING ORGANISMS ON ANIMALS.

Introductory Remarks.—It is self-evident that all animals, without exception, are to a certain degree simultaneously dependent on various other animals as well as on plants; for even such species as appear to depend for their nourishment exclusively on a particular kind of vegetable food also come under the indirect influence of other organisms, often of a great number, by reason of that very limitation. Examples of such highly complicated relations and interdependence are familiar to all, and this relieves me from the necessity of repeating here all that has been said so often and with so much emphasis by Darwin and others on this part of my subject.

Occasionally alterations taking place in these complicated relations may even lead—as is actually known—to the destruction of a species. For instance, if the food-plant supplying a strictly monophagous animal is by any circumstance extirpated, that species must inevitably die out. When plants on which any species of animal is dependent for food are affected and modified by any accidental variation that may occur in the temperature, the moisture of the air, or the nutrition they derive from the soil, the animals living on these plants will

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necessarily be sensible of the changes and possibly perish in consequence. Again, if certain insects whose function it is to fertilise certain plants die out, others living as parasites on those plants would necessarily suffer in a variety of ways. A few species, being wholly monophagous, would perish completely; polyphagous species, as it would seem, might be able to adapt themselves, without suffering in the least, to a changed form of nourishment and mode of life; others again, if they were not extirpated, would probably find themselves affected in some way or other by the change of food, and the effects might very likely exhibit themselves by a certain modification in the structure of their organs. We have mentioned some cases of this kind in the chapter on Food; it will therefore be superfluous to dwell on them here, and all the more so as I have dealt with food as one of the inanimate conditions of existence.

But the reciprocal action of living organisms gives rise to yet other modifications which can be in no way connected with those occasioned by nutrition, even though this may be derived from the organic kingdom. Thus, for instance, there are highly intimate relations between the different individuals of the same species and between the two sexes of a species; many animals are directly dependent upon others, although not using them in any way as food; to these belong the commensals or messmates, which do not feed on their host or on its organs, although they make use of them as a means of procuring the food that suits them.

As a rule the species thus thrown into juxtaposition are reciprocally dependent on each other. If a parasite only destroys the internal germ-gland of its host—as is not unfrequently the case with parasitic worms and crustaceans—the host will not be rendered incapable of living, but only of propagating its species. Thus I have never yet heard of the hermit-crab, *Pagurus*, being found infested with parasitic Cirrhipedia of the genus *Peltogaster* and at the same time carrying eggs on its hind feet; nevertheless, the crabs continue to grow, and are to all appearance healthy. In a similar manner the peculiar larvæ of certain Trematode worms eat away the reproductive glands of pond-snails so completely that they are incapable either of fer-

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tilising or depositing their eggs; in spite of this they live just as well as the individuals not attacked by parasites, and it may be inferred from the size of their shells that they live equally long.[118]

Now, it certainly is a fact that the influence exerted by one living creature over another is in most cases *selective* only. A *transforming* influence, on the other hand, occurs, and can occur, only when the two species come into direct bodily contact. But

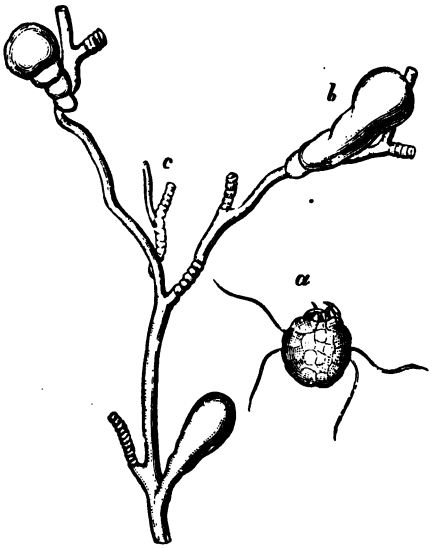

FIG. 85.—Part of the stem (*c*) of a hydroid Polyp, *Campanularia*, with closed pear-shaped galls (*b*) within which lives the larva (*a*) of a sea-spider, *Pycnogonum*.

even then a selective influence is the first to come into play. For example, if a certain species of hermit-crab were an equally good host for the larvæ of all the parasitic Crustaceans which float or swim in the sea, it would in all probability soon be wholly exterminated; consequently the continued existence of the parasites themselves depends not merely on their being able to attach themselves to a suitable host, but also on the selection which the host himself may be able to effect among the guests

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to whom he offers a residence—though he cannot be said to invite them.

The modifying influence of living organisms on living animals.—In a former chapter we have already become acquainted with a case coming into this category; namely, the cysts or galls formed on certain corals by the presence of crabs. In these cases the crabs do not seem to be particularly affected by their host, unless we are disposed to attribute the flat shape of *Hapalocarcinus* or the cylindrical form of *Lithoscaptus* to the direct mechanical influence of their peculiar dwelling-places. The corals, on the contrary, exhibit such great and peculiar deviations from their normal growth that the effects of the parasites on their host are plainly perceptible, both as stimulating and as checking its growth. There are a not inconsiderable number of such cases known. Certain sea-spiders, *Pycnogonidæ*, produce exactly similar galls, but completely closed (see fig. 85), on the stems of a small polyp—as Hodge informs us. All the larvæ of our fresh-water mussels, after leaving the parent, require to attach themselves to the skin of a fish before they can develope any further; there they occasion an excrescence which gradually swells to a capsule visible even to the naked eye, and in this cavity the larva lives for months and goes through its metamorphosis into a true bivalve. We must include in the same category the gall-flies forming galls on extremely various plants.

We are now accustomed, in all such cases of deviation from the normal growth, to regard them pathologically, as the result of disease, and certainly not altogether erroneously, since we know that they constitute more or less frequent exceptions. But supposing that the reciprocal relations between two animals or an animal and a plant were of such a character that each was dependent on the other in an equal degree, so that neither could exist without the other, any deviation from the normal growth must evidently no longer be regarded as indicating disease. We must even consider the apparent abnormity as a peculiarity or character of the species, since it must necessarily occur in every individual of the species. The constancy of the causes which first led to the association of the two kinds of

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animals would inevitably result in the constancy of the deviation, and consequently the transformation of a pathological phenomenon into a normal character would depend solely on the uninterrupted constancy of the active causes. We arrived at the same result when investigating those modifications of structure in animals which were occasioned by the first class of external conditions of life; every variation induced by a change in temperature or nutriment, in the direction or strength of a current, or in the salt constituents of the water, must always recur, and thus become constant or even be increased, so long as the efficient causes remain unchanged. Now, in point of fact, several cases have long been known to us of pathological changes in animals which have become normal modifications, and the causes of which can only consist in the association of two species of animals. I will proceed to investigate these, and a few others which are new or have met with less attention.

A very singular genus of small corals, called *Heteropsammia*, is found living in tropical seas (see fig. 86), of which each individual regularly harbours a worm, *Aspidosiphon*, belonging to the class of *Sipunculidæ*. It is difficult to understand what advantage each animal can derive from their association; yet some must exist, for a coral is never found without a worm I myself have fished up numerous specimens of *Heteropsammia Michelini* in the Philippine seas, and never found one without a worm; and in every representation and description of all the species of this genus, the dwelling of this companion of the coral is always found. Now, the presence of the Sipunculidæ is the cause of certain very conspicuous deviations from the normal structure of the corals they live in—peculiarities which have indeed been regarded and described as specific characters of the species or genus. In young specimens the base of the free-growing coral is scarcely larger than the circumference of the cup; in fully-grown ones, on the contrary, it is much larger. This is the first generic character which appears to be occasioned by the presence of the stranger. For the intruder settles on the base of the quite young coral and grows along with it; but, as it would seem, quicker than the coral, so that the worm, in order not to outgrow the base in its rapid progress, has to curl

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itself round in a spiral. At the same time it appears so to stimulate the base of the coral that it grows faster than the cup itself, and thus the base gradually but conspicuously outgrows the cup. Many corals are affected in a perfectly similar manner by parasitic crustaceans; *Diaseris Freycineti* by certain Cirrhipedia of which the shells often greatly outgrow the foot of the Diaseris, though this too is abnormally extended. Certain species of the genus *Heterocyathus* also are infested by Sipunculidæ just like *Heteropsammia*, and their growth is modified by them. Even in fossil species of this genus holes are often observable in the foot which can scarcely have been anything else than the dwellings of Sipunculidæ.[119] There are also, it is true, some species of the same genus, *Heterocyathus*, which

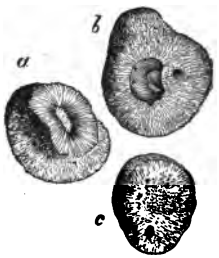

FIG. 86.—*Heteropsammia Michelini*. *a*, seen from above with the broad base; *b*, from below, with the tube of the Aspidosiphon partly opened; *c*, also from below but intact, showing the large entrance of the tube and the small side openings.

establish themselves on the shells of univalves; the animals which have formed these are invariably dead, and the cavity of the dead shell is always occupied by another of the *Sipunculidæ*; but in this last case the worm has had no effect on the growth of the coral, which has followed the normal course of its species and is at most so far modified that the coral, in order to obtain as secure a hold as possible, has extended its base rather more widely over the surface of the shell than seems to be its natural habit.

In the genera *Heteropsammia* and *Heterocyathus*, in the second place, another generic character becomes modified in a very peculiar manner by the *Sipunculidæ*. All the species attacked, of both genera, display both on the under side of the

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base and at the sides a very variable number of perforations which, in all the works that treat of them systematically, are described and particularly pointed out as specific or even as generic characters. But these holes do not in any way agree with the peculiar characteristics of the families to which these genera belong; for in *Heterocyathus* the side walls of the coral ought properly to be quite without perforations, and in *Heteropsammia*, which belongs to the group of corals with porous walls, the holes which we find are quite different from those proper to the coral itself. In both cases these perforations, which are clearly visible in the illustration (see fig. 86), are occasioned by the worm, as is plainly shown by their irregularity of number and arrangement. They open directly into the spiral cavity

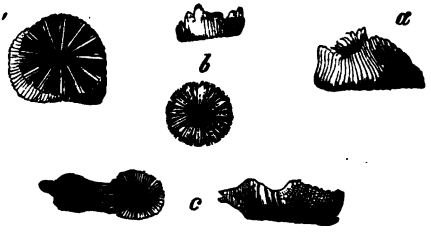

FIG. 87.—*a*, *a'*, *Heterocyathus philippensis*, a fully-grown specimen. At *a* the hole formed by a Sipunculus is visible in the otherwise solid wall of the cup. *b*, a young individual showing the terminal hole of the tube of a Sipunculus; here it is visible in the side wall, but the growth of the coral pushes it to the bottom. *c*, *Heterocyathus parasiticus*, established on a species of *Cerithium*.

in which the worm lives, and correspond exactly to its growth; that hole which is nearest to the opening of the tubular dwelling, out of which the worm protrudes its head, being situated exactly as it must necessarily be with reference to the position of the anus of the worm to serve as a passage for the ejection of excrement. Finally, these holes have no connection with the cavity of the coral itself.

Thus the enlarged foot and the large holes observable at the base or in the sides of the corals, have originated in the same way as those pathological deformities in animals and plants previously mentioned, and this is more particularly proved by the fact that no such holes are formed in the *Heterocyathus*, which establishes itself on the shells of univalves. But as

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they are perfectly constant—no specimen having hitherto been found without such holes, sufficiently proving that a Sipunculus lives as commensal in the coral—they here bear the aspect, or disguise, of a true specific character.

Many years since, a very interesting case of association or commensalism between a mollusc and a coral was described by Steenstrup. The young of *Rhizochilus antipathum* (see fig. 88) have all the appearance and characters of a true Buccinum. When they have reached a certain size they attach themselves to the slender branches of a horny coral known as *Antipathes*, and at once so modify their normal growth that it is quite impossible to name any other mollusc in which any alterations of growth at maturity are to be met with in the least resembling

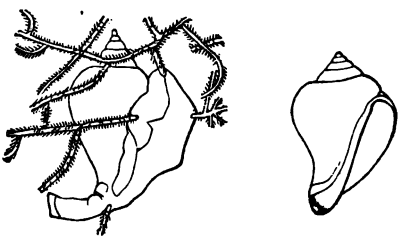

FIG. 88.—*Rhizochilus antipathum*, Steenstrup. To the right the young shell exactly resembling *Buccinum*; to the left the old shell firmly attached to the branches of *Antipathes* by its irregularly formed margin.

it. The shell throws out processes in every direction, by which it clings to the coral, in the mode here shown in a woodcut copied from Steenstrup, till at last the mollusc loses all power of motion and lies, anchored as it were, to the Antipathes. Of what use this can be to the animal it is difficult to say; but we may venture to put forward the hypothesis that it must be, and is, of some service, and also that an originally accidental connection and growth of some true species of Buccinum with the slender branches of a Gorgonia must have given rise to this extraordinary habit.

Certain parasitic Crustaceans offer another example of such a peculiar action of one animal on another. The species of *Peltogaster* often live attached to the hind part of the body of the hermit crab, and they then assume the form necessitated by that

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of their host and of his dwelling. *Pachybdella* lives in preference on the hind part of other crabs, and particularly on the under surface, which, as is well known, the crab always carries folded in under its body towards the front; it occurs almost exclusively on the abdomen of the female crabs. The parasite always (see fig. 12) consists of a somewhat flattened sac, adhering closely on both sides to the surface of the crab's abdomen; the side edges of the parasite, when seen in its natural position, perfectly agree with the form of the crab's body and correspond exactly with the lateral symmetry of the crab itself. The structure of one surface of the Pachybdella almost always differs from that of the other, and one of these surfaces has hitherto been always regarded as the natural hinder side of the Pachybdella and the other as the front or belly; but this is quite an error, as has been proved by the careful researches of Professor Kossmann. The old view seemed quite established by the presence of a large opening which was generally recognised as the mouth, and it cannot be denied that a median line of the body seemed to be indicated by this opening, and by the situation, exactly in a line with it, of a style by which the animal attaches itself to the abdomen of the crab, and these allowed of our dividing it into two symmetrical right and left halves analogous to those observed in most other animal forms. But after Kossmann's observations and an exact investigation of its internal anatomy, previously but little known, there can no longer be any doubt that the flat surface is in fact only one side of the body, and that the two corresponding halves constitute the front and back. Thus, in form, this animal reminds us somewhat of the laterally compressed flat-fishes, in which the back and belly form two edges while the right and left sides are broad and flat; and like them it always lies on one side, sometimes the right and sometimes the left.

I cannot resist the temptation to attempt to explain this extraordinary condition of things by an hypothesis put forward by Kossmann. The larvæ of all the Cirrhipedia—to which Pachybdella belongs—are distinct from those of their nearest allies among the Crustacea by the circumstance that they must pass through a second larva-stage before they can assume the

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form of the fully developed sexual animal; during this stage they have two shells, connected, like those of bivalve mollusca, by an elastic ligament at the dorsal margin. It is probably at this stage that they attach themselves to the abdomen of a crab; this compels the Cypris-like larva to lie on one side, since there is no room for it to occupy a perpendicular position between the thorax and the folded-up abdomen of the crab. Since, moreover, they establish themselves, almost without exception, in the centre of the crab's body, and ere long cast off the hard shells of the larva form, to allow of the growth of the somewhat soft permanent skin, the back and front of the Pachybdella will continue to grow in similar directions, and it is easily explicable on mechanical grounds that the two edges must be symmetrical in their growth, in consequence of the symmetry of the form of the crab's abdomen. In most animals it is not the back and belly that are symmetrical, but usually the right and left side. Now, since the left side of the larva of the Pachybdella is applied to the thorax of the crab and the right to the surface of the abdomen, it need not surprise us to find that the two sides of the body, which in other animals are usually symmetrical, have become dissimilar in consequence of the unusual pressure upon them, and so their normal symmetry is lost. This is actually what takes place, as Kossmann has also proved; the markings and the hairs of the skin of many species of Pachybdella are extremely different on the right side and on the left. This renders the comparison with the unsymmetrical flat-fish—as Plaice—even more striking, but in them the false symmetry of the front and back is less distinctly marked, than in the Pachybdella.

The method here suggested as an explanation of the false symmetry of Pachybdella presupposes, however, that only one individual at a time shall have attached itself to the crab, for in that case only can the abdomen of the crab be capable of pressing the Pachybdella, as it grows, into this particular form. And indeed only one individual is commonly found on each crab. But when—as sometimes, though very rarely, happens—more larvæ than one establish themselves almost simultaneously on a crab's tail, these must mutually hinder each other in the

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form of growth, otherwise determined by the pressure of the crab's abdomen, and we might expect to find that such false symmetry would disappear, since the mechanical causes determining the growth of the Pachybdella would no longer be able to act in the same way. This anticipation is not, however, justified; in the cut here given the abdomen of a crab is shown which bore on it three such uninvited guests, and although a certain irregularity is plainly perceptible in the form and dissimilarity of the three parasites, the false symmetry is quite normal and well developed in all three. This proves that in this case the false symmetry induced by pressure has already become an here-

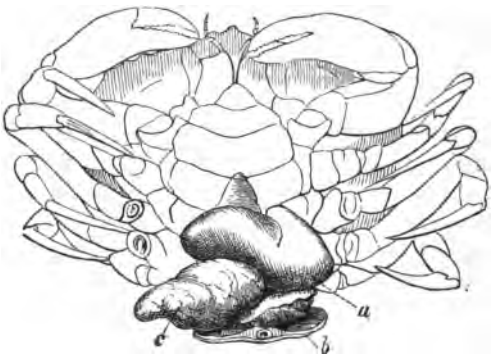

FIG. 89.—A specimen of *Carcinus mœnas*, from Heligoland, with three parasitic specimens of *Sacculina carcini*. All three, in spite of their irregular growth, exhibit the false symmetry proper to the genus.

ditary character of the species; otherwise it must have disappeared. Thus in this case, what was originally an abnormal and pathological character seems to have become a normal specific character, transmissible by inheritance.

A still more wonderful instance of the same kind was long since described by Count Pourtalès. During his dredging expedition in the West Indies he discovered a horny coral (see fig. 90) invariably associated with an Annelid. The worm lives in a tube formed by the abnormal growth—which in this species has become normal—of the slender branches of the coral; they grow together into a rather fine network, and thus form

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a cylindrical cavity lying parallel to the main stem of the Antipathes. Among the numerous specimens found by Pourtalès not one occurred that had not a tube, and thus the same thing has happened here as in the other instances adduced. An abnormal peculiarity caused by a modification in the mode of growth has, by the constant recurrence of the exciting cause, become a distinguishing mark of the species.

In conclusion I cannot refrain from mentioning one more very singular and hitherto little-noticed case of the association of two organisms which seems closely allied to the well-known case of Lichens among plants. These, according to Schwendener's researches, are to be regarded as colonies of true one-celled Algæ and Fungi, and though individual botanists still raise their protest against this view, the latest investigations on

FIG. 90.—*Antipathes filix*, Pourtalès, a horny coral of the West Indian seas, which by constant association with an Annelid has been forced to form a tube for the worm. Deep-sea corals.

the subject seem to prove that they are no longer justified in doing so.

The Sponges are now universally classed with animals; their soft parts consist exclusively of cells which are scarcely ever co-ordinated to form special organs such as occur among the higher animals. These soft portions are usually strengthened and supported by a network of fibres secreted from the cells and extremely variable in structure. In the forms which are generally regarded as the simplest and most typical, all the parts unite to form a funnel attached by the pointed end, and of which the free end has a large opening leading into a central cavity; this, for brevity, we will call the mouth of the sponge. But, besides this, the internal cavity communicates with the surrounding water by a system of fine canals which penetrate the lateral portions of the sponge funnel in every direction. A

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stream of water, produced by the cells of the sponge, circulates through the system of tubes thus formed, and this, it would seem, supplies the animal with food, consisting of microscopic organisms. By a course of growth and subdivision, after the manner of plant-growth, a compound sponge is frequently formed; one, that is to say, which has a number of mouths, more or less, and in which the central cavity—which in calcareous sponges is often quite simple—is transformed into a highly complex structure of internal canals and cavities.

These soft and perfectly harmless organisms, sometimes, however, growing to an extraordinary size, offer a welcome shelter in their innumerable cavities to a host of other creatures, which retire into them, as I might say, for rest and refreshment, and can easily find in their labyrinthine passages a place of concealment from the pursuit of their enemies; sometimes these are true parasites, sometimes only commensals, which establish themselves there. Such a specimen of sponge freshly dredged up from the sea offers to the collector a rich mine of Annelids and Planarians, Nemertidæ and Polypes; Crabs of every kind, various Mollusca, and even Fishes, may be found, and Plants,

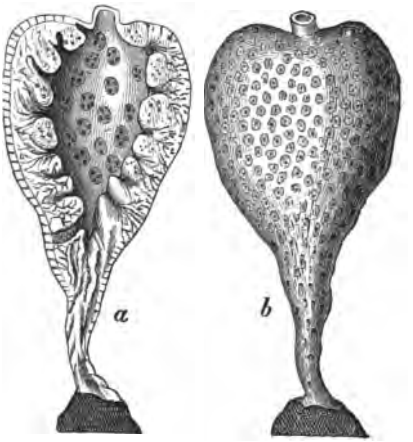

FIG. 91.—*a*, longitudinal section through a calcareous sponge, showing its simple central cavity. *b*, the sponge uninjured. (From Haeckel.)

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as Algæ and Fungi, also establish themselves there. Some of these last have very singular habits; it was Lieberkühn, so far as I know, who first pointed out the fact that certain algæ—the *Florideæ*—are invariably associated with certain species of sponge, and that they grow, not on the soft portions, but on the hard fibres. Other algæ, again, serve as a base for the sponges which cover them like an incrustation. Both of these cases might be designated as instances of parasitism if we knew that, in the former, the Florideæ, living in and penetrating the fibres, derived their nourishment from the sponge; or that, in the second, the algæ supplied food to the sponge growing upon it. But we have no certain information on these points

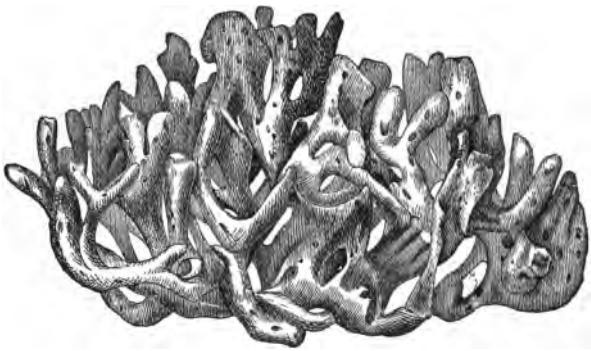

FIG. 92.—*Spongia cartilaginea*, Esper. Half the natural size. The holes in several of the branches are the mouths or stomata of the sponge. By far the greater portion of the substance of the broad branches is composed of the matted filaments of an alga, *Floridea*.

While following up the question as to whether such peculiarities of structure might not in fact be more common than was supposed, and what the nature might be of the reciprocal relations between two organisms thus associated, I unexpectedly met with an object which at the first glance has all the normal appearance of a highly ramified species of sponge. It seems to have been so described already by Esper, and I believe I am correct in designating the organism represented in the cut (see fig. 92) as the *Spongia cartilaginea* of that writer. The branches, which are sometimes cylindrical and sometimes flat, divide in one place and reunite in another, thus forming an irregular net-

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work, with the meshes and branches spreading almost in a plane; such forms are tolerably common among the true sponges. Besides this, all the branches have large perforations on one side, which in living examples—if I may judge from the points of attachment—appear all to be directed upwards. If such a branch is cut across, certain peculiar thick transparent

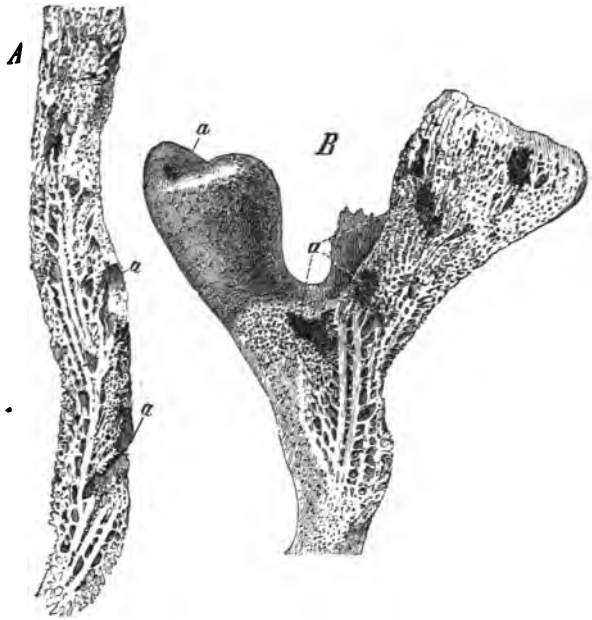

FIG. 93.—*Spongia cartilaginea*, Esper. Sections of branches showing the skeleton formed by the filaments of the sea-weed and the stomata, *a*, of the sponge. The spiculæ and protoplasmic tissue are only visible under a high magnifying power.

fibres appear which do not greatly resemble the usual fibres of sponges, and which penetrate the whole organism in every direction and through all its anastomoses. Still, when we again study the uninjured organism, even with a lens, we feel once more inclined to agree with Esper in regarding it as a true sponge.

But a more minute investigation with the microscope shows

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us, beyond the possibility of doubt, that this body consists of two distinct organisms, namely, of a sea-weed associated with a sponge exactly as is the case with the lichens among plants, and it is impossible, with only specimens preserved in alcohol, and without investigating their vital properties, to decide whether the form of the whole mass owes its origin to the sponge or to the vegetable growth. The thick and somewhat vitreous, transparent branches of the internal network (see fig. 93), which give rise where they anastomose to the broader branches, on one side of which we find the stomata of the sponge, are undoubtedly filaments of a sea-weed—probably an undetermined species of *Floridea*; and the spaces between these internal branches of the sea-weed lead directly into the cavities which, on one side of the main stem, pass into the stomata of the sponge. Hence the margins of these are actually composed of the filaments of the alga. On the other hand, the soft tissue of the sponge proper lies in a very thin layer on each filament; the sponge has no true fibres, though it has spiculæ which are scattered through the soft substance. Unfortunately the spiculæ are so far from characteristic in their structure and their arrangement that it is impossible to determine the genus in which the sponge should be systematically placed. If we assume that its normal growth is neither hindered nor modified by its association with the sea-weed, it may with some probability be included in the family of the *Chalinæ*.

But it is highly probable that in point of fact both the organisms are to a certain degree reciprocally influenced and modified by their association. Although I have examined very numerous examples of these colonies, I have never succeeded in detecting the smallest trace of fructification on the filaments of the Florideæ; they even seem not to grow in the usual manner of the Florideæ, so far as I could determine, and I am supported in this view by those specialists whom I have asked among botanists. In the first place an internal union, by secondary coalescence, occurs between the large primary branches, which continue growing at the ends only; that they are truly coalescent and not merely superficially connected is proved by the fact that in many places the original scar or line of contact is still

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visible, while in others the union has proceeded to such a point that even the cell-walls have merged in one. This appears to me to be a very conspicuous deviation from the normal growth of the Florideæ, for, so far as I know, two separate filaments or branches never, or most rarely, anastomose in these marine algæ. Even the absence of all fructification seems to prove that the sea-weed is forced to an illegitimate mode of growth, so to speak, by its association with the sponge.

But it is, moreover, very probable that the sponge, on its part, is affected by the Floridea. The greater part of its stomata occur only on that side of the broad primary branch which is directed upwards, but sometimes we meet with some which, by a twisting of the branch, have quite lost this normal direction. Now, if the sponge alone could determine the direction of growth, all the mouths would be turned in one direction, and, as this does not occur, the presumption is obvious that this deviation from its normal behaviour is occasioned by the influence of the sea-weed on the sponge. As it would seem, the direction of growth of the stomata is determined by that of the filaments of the alga; this extends its blunt tips—which, as is well known, are its growing points—in every direction. They are found everywhere, at the broad free end of the primary branches, as well as within the oldest portion and all round the mouths of the sponge. As the encrusting layer formed by the sponge is excessively thin, it may be supposed that round about the stomata the growth of the sea-weed is as vigorous as that of the sponge, or even stronger; it is then forced by the filaments of the alga into a direction of growth perhaps not originally natural to it. Be this as it may, in any case the compound organism I have here described must be of the highest interest, and I make no doubt that a careful investigation, not of dead specimens, but of living individuals on the spot, with an inquiry into their mode of life and physiological characters, will furnish an answer to the question whether, as I believe, the organisms—sea-weed and sponge—have a reciprocal influence analogous to that which it has been proved that the algæ and fungi have in the compound organism known as a Lichen.

The degeneration of the organs of parasites.—Besides all

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these influences to which two organisms living in association are exposed, there are yet others which exhibit their results in the degeneration of the organs of true parasites. Most parasites dispense entirely with many organs indispensable to the existence of free-living species; or else they possess them in so undeveloped a state that they appear almost incapable of fulfilling their functions. They are then called rudimentary organs. It is usually said that this extinction of organs which in other cases are so important, is the result of the parasite's mode of life; but this is only a brief way of stating the fact that such extreme degeneration has been observed to any great extent only in those true parasites which actually feed on the juices of their host. The statement is in no way an explanation of the phenomenon itself, and up to the present time we are absolutely unable to assign with any certainty the causes by which, in any individual case, an organ may have been affected in such a way as to reduce it to the rudimentary condition or to cause it to disappear altogether. It is self-evident that all sedentary parasites, or such as live in the organs of other animals, must lead a free life while young, in order to secure the perpetuation of the species by seeking a new host. In accordance with this, we see that all those parasites with the history of whose development we are acquainted, go through a stage of free larva-existence during which the larvæ live under the same conditions as other independent creatures. Such a free existence is, of course, impossible without organs of locomotion, such as legs, fins, and so forth; these again would be useless if they were not under the control of volition and its auxiliaries, the organs of sensation; all these organs must be supplied with nourishment, which the free-swimming larvæ could not obtain unless they had grasping organs to seize their prey; and finally, they could not digest the food thus obtained if they were not endowed with organs proper for that function. Vessels or other contrivances must be present in them which may convey the food-juices to the remotest part of the body; other internal parts must fulfil the task of carrying away all the products of that decomposition of the food-constituents which results from the process of combustion carried on in the

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body, since these waste products are in the highest degree prejudicial to life. Parasites permanently attached to their host and living on its juices have no need of most of these organs, and, in fact, in all such parasites all or most of them have totally disappeared or are extremely degenerate; the degree of degeneration is, however, certainly very different in different species of parasites.

With reference to this it will suffice to select a few of the best-known and more instructive examples from the abundance at our disposal. Among mollusca there is first and foremost the

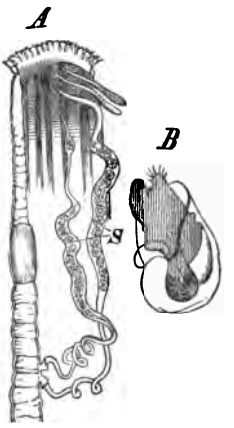

FIG. 94.—*Entoconcha mirabilis*, Müller. *S*, when sexually mature, in the form of a spiral worm-like creature in the body cavity of *Synapta digitata*. *B*, the larva of the mollusc.

well-known *Entoconcha* (see fig. 94); this consists of a simple sac containing nothing but the hermaphrodite organs and the embryos of a univalve mollusc. These embryos have precisely the form and structure of the ordinary larvæ of univalves adapted to a free existence; an oval shell with an operculum to fit the mouth, an organ for swimming—known as the velum, such as occurs in many similar larvæ—a brain and auditory organ, intestines, gill cavity and all the other parts. But all the organs here enumerated are entirely lost when the

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creature is transformed into a mere parasitical pouch-like mollusc living in a Holothurian. The Cirrhipedia, Copepoda, and Isopoda among the Crustacea offer numerous examples of equally extensive degeneration. The extraordinary *Thompsonia globosa*, described by Kossmann (see p. 47), is nothing more than a small perfectly closed sac attached by a short stalk to the leg of a crab, *Melia tesselata*; it contains larvæ in the Cypris-stage without a trace of any other organ whatever, and the other two above-named orders of Crustacea contain several equally degenerate forms. In the same way the larvæ of many parasitic worms are often more highly organised than the fully grown and sexually mature individuals, and in many other groups of animals between those here mentioned 'degenerate metamorphosis' often appears simultaneously with a parasitical mode of life.

Now, at the first glance, it seems tolerably easy to explain the gradual disappearance of many organs in these different creatures by the principle of disuse. We know that a muscle which is not constantly exercised in the proper way gradually loses its power and precision and at the same time materially diminishes in size. The organs of sensation may be rendered keener in their perception by use, and our mental activity increases with exercise and diminishes by lack of employment. Thus, applying this principle to the foregoing cases, we might say that the *Entoconcha* or parasitic crustaceans had lost their organs of motion because, after attaching themselves to their host, they no longer used them. In the same way we might understand the disappearance of a true stomach in *Sacculina* and *Thompsonia*, since it becomes useless from the moment when the animal establishes itself in the cavity of its host and by plunging a sucker into its body is enabled to suck up the absorbable juices of its host, and so to convey them into its own body cavity, without any circuit *viâ* a stomach. Eyes and ears, brain and nerves, muscles and other similar organs, dependent on the will of the animal, might in the same way easily have become extinct from desuetude. But, plausible as all this sounds, certain not unimportant difficulties seem nevertheless to stand in the way of this method of explanation. An investiga-

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tion of these will once more set some of the general principles I have already laid down in a clear light.

If desuetude were invariably to be regarded as a primary cause of the disappearance of organs no longer in exercise, it would be very difficult to understand why, under apparently identical circumstances, identical results should not follow, *i.e.* the disappearance of an organ. All the free-swimming larvæ of the lower Crustacea have similar swimming organs, namely legs, and all alike are thrown out of use by the settlement and attachment of the parasite. In spite of this, the legs are by no means universally absorbed in the same way. In some species one disappears first, in other species another; sometimes too a few limbs are spared and remain attached to the body, though perfectly useless. Hence the same cause affects the same organs very differently in different species; and this proves that the absence of a disused organ is not a mere mechanical result of desuetude, but, on the contrary, is subject to other determining influences according to the peculiarities of the animal whose organs of motion are no longer exercised. We arrived at the same conclusion in a former section when considering the inanimate conditions of existence, and I will endeavour in this chapter to illustrate this point more fully by a few other striking instances.

As a rule a tolerably sharp distinction is made between ecto- and endo-parasites; the former being such as live on the outer skin of animals, *e.g.* the louse, the latter living in the interior organs. It is also regarded as an almost universal rule that ecto-parasites are of less degraded forms than endo-parasites; however, there are some very striking exceptions to this rule. The most remarkable exceptions known to me are the following, which I myself observed in the Philippine Islands.

Holothurians, like all animals, are infested by a great number of various parasites. Besides the *Fierasfer* (a fish) and *Pinnotheres* (see p. 80) which live in the water-lungs, other parasites, molluscs, and worms are found on and in them. Among the former *Eulima* occurs very frequently on the skin of the Holothuriæ (as also on that of Star-fishes); it exactly resembles other univalve mollusca, and its parasitic mode of life

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has only led to its losing the organ for gnawing and masticating which is universal and peculiar to univalves. It does not need it, for it seems to suck up the slimy secretion from the skin of the host. Hence *Eulima* has never been included in the category of true parasites; and rashly dogmatising from this view, the actual observation of Mr. Cuming (the well-known traveller and conchologist), who found similar specimens of Eulima inside the stomach of Holothurians, was at once rejected and explained away by the quite unfounded assertion that the univalves had only been eaten by the Holothurians; but Cuming was perfectly correct in his statement, for I myself have found living Eulimæ in the intestine of large Holothuriæ,

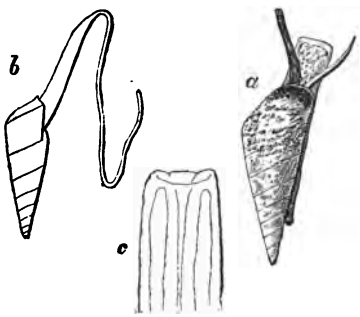

FIG. 95.—Two undescribed species of *Eulima*. *a*, lives creeping freely in the stomach of a Holothurian. *b* is sessile on the skin of a Holothurian, through which it plunges its sucking proboscis. *c*, the front of the proboscis with its simple mouth.

and that very often and by no means as a great rarity. Here they creep about rapidly on their broad foot, on the wall of the intestine, and they have, moreover, all the organs proper to univalves, as a nervous system, organs of sensation, an intestinal canal, &c., exactly like the form living on the outer skin; the only organ wanting is, in the same way, the masticating organ, rachis or tongue, as it is called. With these, certain small flat worms live in the same intestine; these have the internal structure of the Trematoda, but glide along the intestinal canal after the fashion of the Planarian worms, by means of the cilia on their skin; and, lastly, a few species of minute Crustacea, belonging to the Copepoda, float and crawl within

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the intestinal cavity of the Holothuriæ. These have recently been described by Kossmann under the name of *Lecanurius*; but these small creatures have not assumed the organisation of true and degenerate endo-parasites, but possess all those organs which are found in free-living species or in ecto-parasites and which enable them to change their dwelling-place rapidly and at will.[120]

On the other hand, I found on the skin of the very same species of Holothuria which harbours in its intestine the creatures just described, a Eulima which is far more degraded in structure than any other species of the genus. The front of the head which bears the mouth is drawn out into an extremely long proboscis, which pierces quite through the very thick skin of the Holothuria, and the mollusc is just as securely anchored by it as is the Pachybdella by its style or holdfast. But this proboscis must also act as a food-sucker, since it bears, at the end it inserts into its host, a simple mouth without any gnawing apparatus. The foot, which in other species living on the skin is well developed, has here wholly disappeared (see fig. 95), and eyes are likewise wanting. Thus we perceive that the effects usually produced by the condition of living in the intestine, in this instance have not been able to impress the character of endo-parasites on these living in the Holothuria; while, on the other hand, a true ecto-parasite has been modified in the way common to endo-parasites, although it belongs to a group of animals of which the numerous species live, without exception, on the skin of Echinodermata, but nevertheless are thereby modified to so insignificant an extent that their parasitic nature has even been altogether denied.

The causes which have so far come under our consideration as lying within the agency of living organisms and occasioning modifications in animal forms, sink altogether into the background as compared with one now to be discussed, and about which much has been written, and not a little that is false; namely, Hybridisation. This word signifies the fertile union of two individuals which according to our systematic classification are supposed to belong to two different species, and which are supposed, by a certain school of naturalists, never to have been

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intended by nature to be capable of actual sexual union. Hence the opponents of Darwin's theory—maintaining, as they do, the immutability of species—have always denied the occurrence of hybrids, or have declared that even if they could occur the offspring of such an unnatural union must inevitably prove barren, or, finally, that the fertility of the progeny of a successful case of hybridisation affords a proof in itself that the animal forms previously regarded as distinct species must henceforth be considered a mere variety of the same species.

The importance of the subject induces me to pass the facts briefly under review.

In the first place, it must be stated that those persons who deny, even now, the general possibility of hybridisation, by that very denial display their ignorance of the subject. It is simple folly, in the face of the increasing number of cases of successful hybridisation in our Zoological Gardens, to insist on maintaining this negative position. Hybrids are already known to us in the most widely dissimilar classes of the animal kingdom. Among apes, *Cynocephalus mormon* and *Macacus cynomolgus* have crossed and produced young; the hybrid race of Leporidæ, a cross between the rabbit and the hare, is very generally known; the tiger has bred with the lion, the leopard with the jaguar, the polar bear with the brown bear, the masked pig with the common Berkshire pig, *Dama vulgaris* with *Dama mesopotamica*, *Equus onager* with *Equus hemippus*, *Equus Burchelli* with the common horse, and then again with the common ass and *Equus hemionus*, and all these crossed couples have repeatedly given birth to offspring. Quite lately a hybrid snake was born in the Zoological Gardens in London, a cross between *Chilobothrus inornatus* and *Epicrates angulifer*. Among ducks hybrids are extremely common; *Anas sponsa* crosses with *Fulicula ferina* and *nyrocca*, *Anas boschas* with *Anas crecca*. Among fishes hybridisation between two species of carp or of trout is very easily effected.* Hybrids of invertebrate animals are less common; this, however, may be because they have been less experimented on by man, or because they have generally attracted less attention than the vertebrata.

* *Salmo salvelinus* and *S. fario*; *Cyprinus carpio* and *C. carassius*.

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Among insects, however, there are several species known which readily breed together and produce hybrid offspring; thus a cross has been produced between the larger and smaller peacock moths and between the willow and the poplar hawk-moths. I have intentionally mentioned here only some of the more recent cases (there is a mass of well-established older examples which may be found briefly enumerated in the fourth edition of Claus's 'Lehrbuch der Zoologie').[121]

This must suffice; the fact that two different species can unite and be fertile must be regarded as established, for in most of the cases here enumerated the individuals breeding together stand so far apart in the systematic scale that no systematic zoologist—not even the most virulent anti-Darwinian—could venture to assert that they were only varieties of one and the same species.

However, to deprive these numerous instances of hybridisation of any universal application and value, it is further asserted that the newly originated hybrid forms are always, or almost always, sterile. But even this statement must be declared to be inaccurate in its naked and literal form. The race of the Leporidæ is, as is well known, perfectly fertile, and has produced other cross-breeds with both the rabbit and the hare. Hybrids between the dog and jackal or between the dog and wolf remain fertile for many generations; those of *Phasianus colchicus* and *torquatus* are perfectly fertile; so are the well-known hybrid geese, and those between *Cervus vaginalis* and *Cervus Reevesii*; a female mule in the Jardin d'Acclimatation at Paris has produced two foals to a horse and two to an ass; in the Zoological Gardens (London), a hybrid female of *Bos indicus* has had young by a male of *Bos frontalis*. Newton states that a hybrid female between the common duck and *Anas boschas* proved fertile with a male *Mareca penelope*, and I have no doubt that many similar cases have escaped my notice. The infertility of hybrid races is certainly not a universal law, for besides those cases which are always, or under certain circumstances, infertile, we meet with others, as we have seen, not less numerous, of which the undiminished fertility is undoubtedly established by reliable observers. We may conse-

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quently assume it as proved that cross-breeds *may* originate from hybridisation which are both fertile and capable of transmitting their characters to their descendants, but that certainly there is no *must* in the case.

An attempt may, however, be made to invalidate this position by the assertion that, although the formation of such hybrid races may be possible, it can only succeed with domestic animals, and never in the freedom of nature and without the co-operation of man, since in all the examples here adduced the cross-breeding has been intentionally effected by man in animals kept in captivity. I may at once admit that though I have so far mentioned none but such cases, it is not because cases of hybridisation in a state of nature have not been observed; I have purposely reserved the mention of them, and will now first briefly allude to some rather doubtful examples. *Felis torquata*, described and correctly drawn by Cuvier as a distinct species, appears to be a hybrid, produced in a free state, between the domestic cat and *Felis bengalensis*; *Anas bimaculata* is a freely engendered hybrid between *Anas boschas* and *Anas crecca*; *Tetrao medius*, in the same way, between *T. urogallus* and *T. tetrix*. Siebold's view is certainly well founded, that the vast number of intermediate forms which constitute the *crux* of the zoologist who endeavours to determine the species of the fresh-water fishes of Germany, must have originated from cross-breeding in a state of nature; this naturalist, in his well-known work on the fresh-water fishes of Germany, enumerates no less than eight hybrids, most of which have been described by other zoologists, even as types of special genera. According to Von Loewis, *Lepus timidus* and *Lepus variabilis* not unfrequently produce hybrids. Dr. W. Wurm states that he has often seen cross-bred partridges. J. von Fischer * asserts that the polecat and ferret are two different species and produce hybrids in a free state. The case noted by Mr. Buxton is perfectly verified, of a male white cockatoo and a female rose-coloured Leadbeater's cockatoo, which had never bred in confinement, and which when set at liberty in the woods near that

* Director of the Zoological Gardens at Cologne. His sketches of animal life are well known in Germany.

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gentleman's house bred two years in succession. The processes of such attempts at hybridisation have not unfrequently been detected. Thus, G. Koch observed the union of *Zygæna peucedani* with *Zygæna trifolii*, of *Zygæna minos* with *Zygæna loniceræ* and of *Smerinthus populi* with *Smerinthus ocellata*. A. Meyer detected that of various species of *Phryganidæ*; Peragallo that of *Luciola lusitanica* with *Ragonycha melanura*; Kuenckel that of *Strangalia melanura* with *Leptura livida*; Gerstaecker that of *Tipula oleracea* with *Pachyrhina scalaris*. Heynemann also tells us that *Limnæa stagnalis* and *Limnæa auricularis* have bred together. Of course the question remains unanswered as to whether in all these cases the union led to the production of offspring; but the mere fact that in a free state of nature such attempts at hybridisation are certainly made, renders it in a high degree probable that they may frequently lead to such a result, and we can no longer doubt the possibility of hybridisation in a free state of nature.

Now, I began by saying that such hybridisation might be one of the means employed by nature for originating new forms, that is to say, for producing offspring, and, moreover, fertile offspring, which varied from their parents in form, colouring, and other characters, thus offering to Selection fresh material to experiment upon. To justify this statement it will be sufficient to examine one or two of the above-quoted instances rather more minutely.

The hybrid cockatoos which I have mentioned were distinguished from their parents very conspicuously, for while one of these was white and the other rose-coloured, both the broods of young birds had large orange-coloured tufts. All the hybrids of fishes spoken of by Siebold display a peculiar mixture of the characters of both parents, besides others which cannot be referred to either with any certainty. The descriptions given by many systematic naturalists of recognised ability, of various hybrids as distinct species, prove that n these cases—as, for instance, in *Felis torquata*, *Anas bimaculata*, and others—characters occur which do not positively belong to either parent. The hybrid between the masked pig and the Berkshire pig was lack with white feet, and the hybrid bear born at Stuttgart,

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which was recently described, the offspring of a cross between the brown bear and the Polar bear, is described as follows.* 'The change of colour undergone by the hybrid young was very interesting. All four came into the world quite white, but presently assumed a silvery grey or bluish hue, and at the age of three months were of a dark-brown colour, shot, as it were, with a blue gleam. They at no time showed any trace of the white necklace which is characteristic of the young of the brown bear. The two that are six months old are at present for the most part greyish-brown, but not uniform in colour; all about the throat they are conspicuously lighter, almost white. The two that are eighteen months old are much lighter altogether; the backs and sides are a light bay-brown; a dark median band in one of them is tolerably broad and extends all down the back; in the other it is only faintly indicated in the fore-part; the top of the head is light brown, the under part and the rump whitish, all four extremities a rather dark brown.' It is easily seen from this description that in this case changes in the colouring have been produced in the hybrids which exhibit a very considerable deviation from that of the parents.

At the same time this last-mentioned instance is particularly adapted to bring into prominence another phenomenon which is at least as conspicuous in the hybridisation of animals as of plants, namely the mixture in the hybrid young of the colouring of both parents, particularly in the hybrids of insects and birds. In these a very distinct combination of part of the colouring of the female with differences taken from the male is regularly reproduced, as the mixture of colours in the hybrid (or mule) of the canary-bird and goldfinch; in the hybrids above mentioned, between the poplar and willow moth, the peculiar marks on the hind wings of the former may be plainly seen overlying the eyes of the latter. But the extent of this mixture is extremely different in the individual progeny, as has been evident in the minute description of the hybrid bears; sometimes the colours of the female predominate, sometimes those of the male, and this may occur in different young of the same brood. Thus it is evident that hybridisation does not result merely in an aggregation

* In a German periodical, 'The Zoological Garden.'

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of new characters in addition to such as are already present in the parents; but these too are rendered to a certain degree fluctuating, so that any exact, or even approximate, repetition of them in the offspring is put out of the question. The rigid constancy of the parental characters maintained by interbreeding is so completely interrupted by hybridisation that the organisms thereby exposed to the means of selection acting on the young animals are to a certain extent perfectly new. Certainly, we as yet know very little concerning the mode in which hybridisation affects any other characters than the colouring; the comparative difficulty of breeding such hybrids, and the short series of years that have elapsed since more attention has been paid to such cases than formerly, leave no room for surprise that available material is so extremely scanty in this direction. But this cannot alter the results that have been attained so far; for if after longer investigation we should be brought to the conclusion that in the animals at our command for experiment the colouring of the skin, or of its covering, still seems especially adapted to exhibit the effects of hybridisation, while other organs as the skeleton—for instance—are not affected at all, or in a very insignificant degree, neither of the principles above laid down would be disproved, but merely restricted in their application.

If we now compare and contrast inbreeding and hybridisation—cross-breeding—it is well known that the very essence of the former process is the union of very closely allied individuals of the same race or species, while that of the latter, on the contrary, is the union of individuals very distinct from each other. And since this contrast, so far as we learn from the numerous experiments now within our knowledge, points to one and the same cause as that by which the difference in the results of the fertile union is determined in each case, we may deduce another general principle which will lead us to still wider conclusions: namely, that the more remote the systematic affinity is of two animals that unite to produce young, the greater is the probability that, together with a perfectly undetermined mixture of the parental characters, new characters may arise which do not occur in either parent. The cause of the disturbance thus arising in the constancy of the specific character is the act

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of sexual union. Hence we may further infer that sexual union is in itself an auxiliary to the interruption of the constancy of species, even when it is effected between two individuals of the same species; only in this case it is worked out by nature with far less violence, as I may say, than in cases of true hybridisation. And this agrees with the results of investigation in the domain of botany, for Sachs, in his 'Text-book of Botany,' expressly says that there is no essential difference between the self-fertilisation of pure species or varieties, and fertilisation by other species or varieties, and that in the case of true hybridisation many peculiar characters attributable to sexual differentiation and agreement are brought into greater prominence. From all that we know at present the interruption of the constancy of specific characters may be regarded as one of the most conspicuous of these peculiarities.

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CHAPTER XII.

THE SELECTIVE INFLUENCE OF LIVING ORGANISMS ON ANIMALS.

In the foregoing chapter we have seen that two organisms coming into physical contact may be able to exert a permanent transforming influence over each other. But this purely mechanical transforming or modifying process must always have been preceded by selection; for if all the larvæ which creep or swim on the earth or in the water were equally capable of settling on any plant or animal that accidentally came in their way, these species would certainly be extirpated. Thus, in order that such animals may continue to exist as are capable of affording shelter or food to a certain number of others, they must be enabled to make a selection between the species which crowd upon them as commensals or as parasites. This selection may under some circumstances have been already effected by the other conditions of existence, as we saw in the first section; but a second process of selection may be performed on those forms which have been able to outstep the limits thus imposed upon them, by the animal they choose to settle upon. This is of course always undesigned. A very striking example of this selective power of individual animals on the larvæ of parasites is offered by the different forms of the family of the Bopyridæ among the Crustaceans. Many of the species, and particularly those of the genus *Bopyrus* (see fig. 38), live in the branchial cavities of crabs or of tailed Crustaceans, in which they always produce an enlargement—sometimes a very considerable one—of the branchial cavity. We may suppose that the young larvæ pass into it with the current of water which enters the branchial cavity close to the mouth to supply the gills with fresh water,

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for there is no other and certainly no more convenient way. This stream enters both the gill-cavities at once; it is therefore easy to understand that the larvæ sometimes get into the right and sometimes the left cavity, and also that in the course of their growth, which is probably very rapid, they must hinder other larvæ from settling in the same spot, or perhaps they feed on the later arrivals as an easy prey. But it is highly remarkable that when one individual has established itself in one branchial cavity it is impossible for another animal of the same species to settle in the other unoccupied gill-cavity; so at least we may conclude from the fact that hitherto no case has been described of the simultaneous occurrence of two individuals in the gill-cavities of the same Crustacean. I myself, though I have collected and studied hundreds of these animals, have never met with one exception to this rule, and my observations have been confirmed by so distinguished a student of the natural history of Crustaceans as Professor Gerstaecker.* So far as I can see, there is only one possible way of explaining this striking fact. The guest already in possession of one of the cavities—let us say the left—cannot of course directly prey upon or turn out the larvæ brought by the current into the other unoccupied cavity; it can only do this indirectly, by so influencing its host that after the establishment of the first intruder it is no longer fit for the reception of a second.[122]

Where, as in this case, the two different animals do not come into actual contact and yet exert a definite influence on each other, this under all circumstances can only be a selective action, and this selection, as is well known, may be effected in a variety of ways. With regard to the end I have in view, it would be superfluous here to discuss all or even most of these ways; the general result will be set in a full light by considering a small number of examples. But before we more closely examine the means which nature has bestowed on animals to give them the advantage in their relations towards others, it will be desirable to say a few words in general consideration of those mutual relations of any two animals which are called forth

* The well-known editor of the section on Crustaceans in Bronn's great work on General Zoology.

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by their respective struggles for the same conditions of existence.

The competition for similar conditions.—It is self-evident that different animals, or different individuals of the same species, must often come into antagonism in their search for food or for other things. In such cases the struggle will be the severest when they belong to the same species; for as they then will have approximately the same aims and about the same strength, skill, and powers of resistance, the combat for the hunting-ground, the female, or for dead prey must be more severe than when the antagonists, belonging to different species, have in consequence different needs and tastes, and exhibit a conspicuous difference in their strength of body or in their weapons of offence and defence. In the latter case even, under certain circumstances, the struggle to obtain possession of the same object may come to an issue without any personal combat; for if the two creatures attack the prey in a different manner both may be satisfied before they come into collision, and a personal combat will be averted. When, on the contrary, two individuals of different species can apply the same, or nearly similar, means for appropriating and keeping possession of the booty, just as virulent a contest must ensue as between two individuals of the same species.

Any such direct battle between two animals, whether of the same or of different species, must always result in selection. The phrase 'Survival of the Fittest' is a happy one, but it is a somewhat rough and not perfectly exact expression of the outcome of such cases; for it is certainly not always the fact that a species which is not qualified to conquer in such a personal contest with one species not its own, must be equally incapable of triumphing in a struggle with another, and so inevitably perish. This could be the invariable result of such a struggle only when the life of an individual or the existence of a species depended solely, and in every particular, on those conditions which had occasioned the strife of the two combatants.

But, besides this, as has already been remarked on many sides, this selection by direct personal combat does not depend, as many imagine, exclusively on it and on the mode in

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which it is more or less successfully conducted by this or that individual, but also on the reaction of those very conditions for the possession of which the struggle took place. An example will here be appropriate. Supposing that two suitors of the same distracting beauty agreed to fight a duel for the possession of the fair one, the surviving lover could be designated as fortunate only in the event of its having been understood that he would thus win the lady's affections. This example illustrates, with a little exaggeration of course, the indisputable fact that in every case of a competition between two animals for one and the same object, this object itself must have a certain, and indeed a selective, influence on the ultimate results of the contest. Supposing that two larvæ of dissimilar species of *Bopyrus* should meet at the entrance of the same branchial cavity and begin a struggle for the possession of it, under certain circumstances the parasite to which the cavity did not properly belong might come off victorious, but this would avail it but little, since it could not live in the branchial cavity of which it had obtained possession. The larva of an insect boring and living in wood might perhaps in the same way be able to conquer another which was accustomed to live and bore in leaden bullets; but it is extremely doubtful whether the wood-borer would thus be enabled to live in the lead. Exactly the same thing occurs between two individuals of the same species. We might perhaps be inclined to assume that the tendency of two individuals to possess themselves of the same object was of itself a satisfactory and sufficient proof that both animals must be equally well fitted for the condition of life in dispute, but nothing could be further from the truth than this assumption. If, for instance, two men contend for the same office, a presidency or a professorship, under all the given circumstances one will be better fitted for the post than the other, and if among men this better qualification were the sole condition of selection the post would always be filled by the best candidate; the post itself would effect the selection by the qualifications which it demands. It is precisely the same with animals. When two lions or wolves fight for a prey, the stronger will undoubtedly win; but if the conqueror happens to have a bad digestion, in

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spite of his victory he will not be able to derive the same benefit from it as the weaker might have done in the same circumstances.

The capability of an animal for winning a suitable position in life can never depend on one qualification alone, as for instance the possession of powerful weapons. If we suppose that all the Nauplius-larvæ of a Pachybdella were simultaneously produced, and that they consequently all started simultaneously on a race for their place on the abdomen of a crab, the victory would naturally rest with the best swimmer. But the very organ which had secured it this success would subsequently be of no further use to it, since its powers of attachment and therewith its final success in life depend on the clinging antennæ of the larva. Supposing, then, that the individual arriving first were ill-furnished in this respect, all the benefits of the victory would be lost to it, since the crab might possibly be able, by a vigorous movement of its hinder parts, to get rid of the unwelcome guest. If the conquered laggart and inferior swimmer were to arrive at this moment, and if it possessed better organs for clinging than the foremost one, it might, though originally beaten, finally become the possessor of the field—on the abdomen of the crab.

Thus the selection effected by the issue of a direct combat for any particular condition of existence can only lead to further results when the surviving party is also qualified to secure the benefits of the victory. This point, as it seems to me, has not seldom been lost sight of by Darwin's followers, and still more by his opponents, who have frequently designated direct combat as the only means of selection. Darwin himself, I am perfectly convinced, never meant to say that a direct struggle between two individuals was the only or even the most important means of selection made use of by nature in the process of natural selection. Nevertheless, the struggle for existence cannot but be rendered more severe by the occurrence of such personal combat than it already is; and since this will chiefly occur when the individuals are as nearly alike as possible, it must, no doubt, very frequently be a means brought into play by nature to effect a selection between several varieties of the same species

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lying at her disposal for the end and purpose of forming a new species. But this must depend not only on the reaction of the object or condition fought for, but also on the qualifications which the individual—or the variety—brings into the contest; and it will be advisable here to examine somewhat more closely the relations thus originating between different animals.

The relations of the pursued and the pursuers.—The means adopted by nature to give one form the victory over another are endless in variety. Muscular strength and powerful natural weapons give the advantage in some cases; swiftness of limb, nimbleness and skill in others. Neither cunning nor instinct, nay, not even really intelligent characteristics, are always capable of contending successfully with antipathy or sympathy; persevering inactivity or even overweening stupidity sometimes secures a great advantage in such a contest. The proverb is a familiar one, 'The gods themselves cannot contend against stupidity'—a firm belief in any dogma, be it the most stupid in the world, gives it a certain power and affords its adherents the confidence they need under the attacks to which it is subjected. The weak or the timid will often find a protection in the semblance of courage which they may be able to put on. In short, there is no quality of body, of mind, or of instinct which may not, on occasion, prove a powerful weapon of offence or of defence. The very various external weapons used by animals in personal combat are familiar to every one. One species uses its teeth, another its feet, or both together, like the elephant; the bird uses its bill, wings, or legs and spurs; the apparently ponderous horn on the nose of the rhinoceros is a formidable weapon, and the rattlesnake has one no less dangerous at the end of its tail; the abdominal glands of scorpions and ants, or the poison glands in the mouth of venomous snakes and in the maxillary glands of spiders and centipedes, the fœtid oil-glands of many caterpillars, of bugs and beetles, and of many fœtid species among the Vertebrata, are all so many weapons available alike for defence or attack. Many of them—probably by far the greater number—are very constant in their occurrence, and in their structure, size, and form; other characters, as those known as secondary sexual characters, particularly in insects,

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are frequently very variable in their peculiarities. This last circumstance has given rise quite recently to an objection to the applicability of Darwin's principles which I will here take the opportunity of discussing briefly.

Kramer asserts, on the ground of a very elaborate mathe-

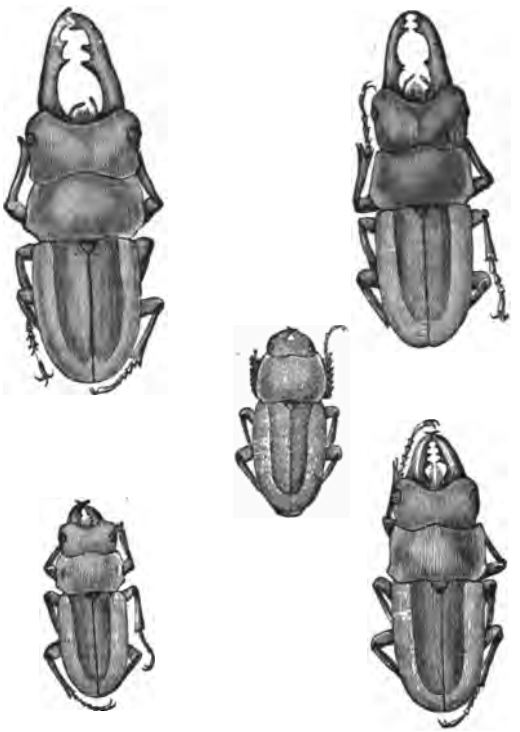

FIG. 96.—*Cladognathus dorsalis*, Erichson. In the four corners are four different forms of the male; the lower form on the left has mandibles hardly larger than those of the female in the middle. Natural size.

matical calculation on the method of the doctrine of chances, that, assuming Darwin's principles as the basis of such a calculation, the extreme forms of a series of varieties must be less numerous than the intermediate forms, and in the same way that the production of excessive deviations must also be possible;

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the result would be a chaos of male forms gradually passing into each other and all belonging to a single female form. And he adds that this result, mathematically calculated, stands in trenchant contrast to the facts, for it is known on the contrary that the secondary sexual characters of male beetles, in by far the greater number of cases, are extremely constant.

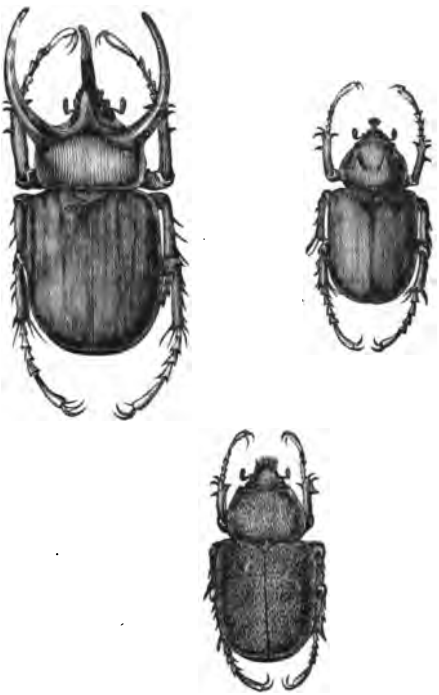

FIG. 97.—*Chalcosoma atlas*, from the Philippines; the upper one to the left is the horned form of male (*C. Atlas*, Linn.), the upper one to the right is the almost hornless form (*C. Phidias*, Blain.). Below is the female. Half natural size.

But Kramer has not taken one element into his calculation which ought, under the circumstances, to have been duly considered; he calculates only the results of an unlimited capacity for variation in the males, while it is precisely this variability which, according to Darwin's views, will be limited by sexual

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selection, though not wholly prevented. Thus Kramer's calculation only holds good for those cases in which the causes that gave rise to the occurrence of deviations from the parent species continue to act unchecked and uniformly, and alone determine the final result. He denies, indeed, that such cases can occur, but, as it seems to me, without reason. For, particularly among tropical species, there is a not inconsiderable number of such instances, one of which is exhibited in the accompanying cut (see fig. 96) of the extreme forms of the male *Cladognathus*. Here, according to my enumeration, the varieties standing about midway between the two extremes represented occur in by far the greatest numbers; towards each extreme the number of individuals gradually diminishes, till at last, of the two extreme forms only one of each was captured among hundreds of others.

The Lamellicornes in general, beetles with flat leaf-like antennæ, exhibit a marked difference in the form of the two sexes; the males very frequently have large or small horns on the head, while the females are usually devoid of them. This is most conspicuous in the Goliath beetles, as they are called, of which many species are very common in the tropics. Sometimes the horns of the males vary in a quite extraordinary degree; as an illustration I here subjoin the extreme forms of the male of *Chalcosoma atlas*, a species mentioned by Darwin (see fig. 97); one form is the original typical *Chalcosoma atlas*, of Erichson, the other, smaller one, *C. Phidias* of Blainville. I have captured many hundreds in the Philippine Islands, and from among them have selected the two specimens here accurately drawn from nature. They are the two most extreme forms of a quite distinct series, and I can positively assert that they are both of the same species. It can be seen that the larger individual has four large horns, one of which belongs to the head and three to the prothorax; the smaller specimen shows only a trace of the horn on the head; the middle horn on the prothorax has disappeared entirely, while the two lateral horns are not merely absolutely smaller, but much smaller in proportion.

Darwin has adduced similar cases, and not only of insects, as Kramer seems to suppose, but of Crustacea, Spiders, Birds, and

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Mammals. All these examples consequently display, in a conspicuous degree, those very phenomena on which Kramer calculates, but with the omission of an essential factor, namely, that very factor which, according to Darwin, is, under the form of 'sexual selection,' one of the chief agents in effecting the selection, *i.e.* the preservation of extreme and particularly favoured varieties. If, on the other hand, we take this factor into the calculation, the numerous cases so strongly insisted on by Kramer, of great constancy in the distinctive characters of male beetles, may be very well explained by Darwin's principles. According to these the selection effected in these instances by the physiological bearings of the organs in question has already acted, and has selected, and consequently rendered constant, those species which had special advantages in the struggle which led to the selection; while in those cases of still prevailing variability for which Kramer's calculation holds good, no such physiological bearings can have been at work. For it must not be forgotten that neither natural nor sexual selection can originate new characters, but can only come into play when some active mechanical causes have given rise to such modifications in organs already existing, as are capable of introducing some new physiological correlation. So long as this does not take place, the force which originally gave rise to the deviations, *i.e.* the variability, will still be able to act unchecked. Now the question as to how an old organ may come to have a new physiological value, in relation either to the other organs of the same creature or to the external conditions of existence, is evidently one of great importance; and this seems to me a suitable opportunity for studying it with reference to an actual example, namely, the eyes recently detected by myself on the back of an *Onchidium*, a naked mollusc.

It is universally known that almost all univalve Mollusca have two eyes either at the tip of the tentacles or at their base. These eyes are extremely different as to structure from those of the Vertebrata. In all eyes, without exception, the optic nerve is gradually merged in a layer of tissue which includes the terminating fibres of the nerve and is known as the retina; these fibre ends are the rods and cones, or columnar layer. In Verte-

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brata (see fig. 98, *b*) the optic nerve penetrates the outer skin of the eye, and spreads out on its inner surface between it and the lens in such a way that these ends of the nerve are turned away from the lens and thus have their free ends directed outwards.

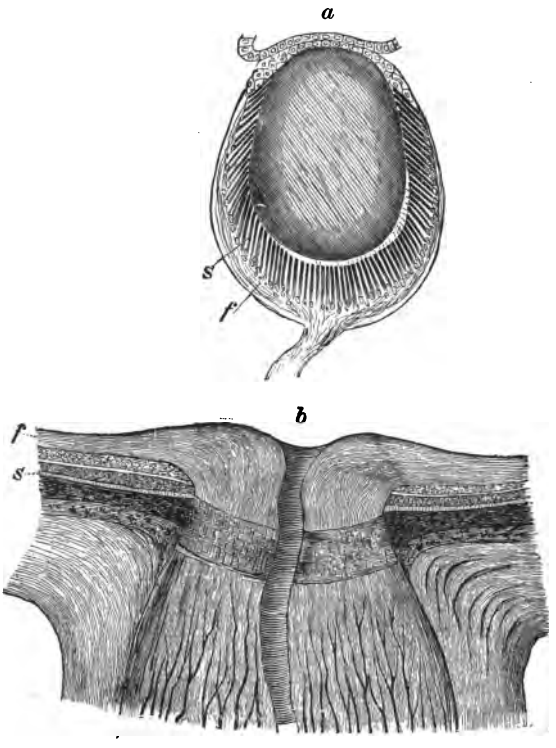

FIG. 98.—Sections of eyes (*a*) of a univalve. *s* is the layer of rods and cones enclosed in *f*, the fibrous layer of the retina. *b*, the eye of a vertebrate animal at the spot where the optic nerve enters it. The nerve traverses all the layers and spreads out, forming the fibrous layer *f*; the columnar layer lies outside it, and thus in the reverse position to what it occupies in the eye of the mollusc.

In the eyes found on the tentacles of snails (see fig. 98, *a*) these rods are in the contrary position; the surface of the tips is turned towards the lens. Thus, in the former, the layer of rods and cones itself is pierced by the optic nerve, and in that spot of

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course none can be formed; hence vertebrate animals are blind in that particular spot, which is in fact known scientifically as 'the blind spot.' Such a spot is absent in the eyes of the second category; the optic nerve extends over the outside of the eyes, and the rods and cones situated within cover the whole inner surface of the retina uniformly.

So far as concerns the eyes placed on its head the genus *Onchidium* in no way differs from the allied groups. But the greater number of species in this genus are further distinguished by having other eyes situated on the shell-less but coriaceous

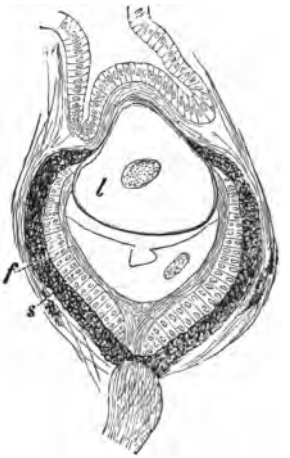

FIG. 99.—Section of the dorsal eye of *Onchidium verruculatum*, letters as in fig. 98.

back of the animal. These dorsal eyes (see fig. 99) are extremely interesting, for, simple as they are in structure, they are identical in type with those of the vertebrata. A comparison of the two sections here given of the eye of a vertebrate animal and of one of these dorsal eyes will suffice to exhibit the resemblance; in both there is the 'blind spot,' because the optic nerve must pierce the external layer of the retina; and in both the layer of rods and cones forms the outer layer of the retina. This is the only example hitherto known of an eye so constructed in an invertebrate animal.

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It is evident that these eyes must be of the greatest importance in the life of the animal possessing them. In the first place it is simply inconceivable that well-developed eyes, capable of fulfilling their functions, should be useless. If eyes occurred in other univalves in the same place as in Onchidium, we should naturally think at once that the dorsal eyes of Onchidium were degenerate eyes; but they are found exclusively in this genus, whence we may infer with considerable confidence that they must have originated in it. But supposing they were, nevertheless, rudimentary eyes inherited from extinct ancestors [123] of this family, they must in some way prove themselves to be such; we should expect to find some part absent—the lens, or the rods and cones, or the pigment of the retina. All these parts, however—recognised as being essential to the normal use of the eye—are present in the dorsal eyes of the Onchidium, and not in one species only, but in above twenty forms that I myself have examined. Finally, all these twenty different varieties of dorsal eyes represent an unbroken series, from those of very low development up to the highest, and they all exhibit the essential parts of a seeing eye, varying in arrangement, it is true, but quite normal in structure. This irrefutably proves that these eyes have originated independently in the family of Onchidiadæ, and that they are no doubt of great importance in the life of the mollusc.

During many years of travel in tropical regions these eyes were perfectly unknown to me; but on other grounds I had devoted much attention to the mode of life of the Onchidia. They live exclusively on the seashore or in brackish marshes; they creep along close to the edge of the water, hiding in clefts of the rocks or under large stones. Together with them, in the same spots, live numerous specimens of two genera of fishes, *Periophthalmus* and the nearly allied *Boleophthalmus*; these skip along the strand with long leaps, evidently seeking their food, which, besides insects, consists principally of this very genus of mollusca. This, as it seems to me, affords a way of accounting—though only hypothetically, it is true—for the development of these dorsal eyes. The Onchidia are terribly slow creatures, perfectly incapable of escaping or of withdrawing

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rapidly into a rift for shelter. They eat nothing but sand, which they shovel into the gullet through the mouth, as do some of the Echinoderms; of course they only digest the nutritious organic particles which are mixed with the sea-sand. Thus, in order to find suitable nourishment, they must often be exposed to the gaze of the swift fish that leap rapidly along the edge of the sea, as well as to that of other animals. Flee they cannot; a house into which to creep—like many other molluscs living equally exposed—they have not; they have neither spines nor jaws with which to defend themselves; and the eyes on their back, which are capable only of warning them of the approach of danger, do not avail to provide them with protection; in short, even with these dorsal eyes they

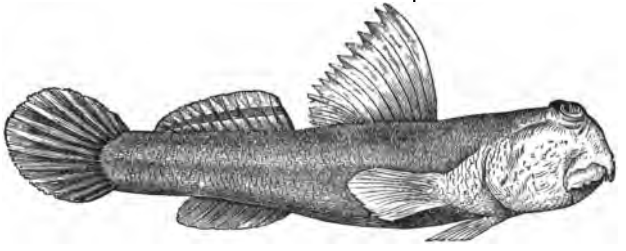

FIG. 100.—*Periophthalmus Koelreuteri*, a fish which pursues Onchidium—a land mollusc—on the sea-shore. The large ventral fins serve for a forward leap.

seem to be perfectly defenceless against their pursuers. Still, it would certainly be very strange that such eyes should be developed here, and only in this particular genus, without being qualified to be of any real advantage to them, since they certainly cannot require eyes on their back—useful, no doubt, for looking up to heaven, but quite useless for looking down on earth—in order to find their food, which lies close before them in the sand under their mouth.

Hence, if these eyes were in fact to be of some service to the mollusc, it must have been also provided with some sort of weapons, and in point of fact such weapons do exist in every species that has such eyes. The skin of the back is very thickly set with minute glands, of which the contents are not perfectly

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fluid, but rather a kind of concretion, and the pores for its emission are excessively fine, so as to be hardly discernible. Moreover, these are closely surrounded by a circular muscle, so that by its contraction the openings of the glands are easily closed. Feeble contractions of the skin, such as inevitably occur in the act of creeping, cannot consequently express the minute globules of the secretion out of the glands; the moisture cannot exude. But supposing that a Periophthalmus approaches suddenly and with rapid leaps (see fig. 100); it rises—as I have often seen—several inches into the air, and may thus not unfrequently throw a shadow from some distance off, on the back of the slowly creeping Onchidium, and of course alarm it greatly. The mollusc has all its eyes—and I have positively counted ninety-eight on one specimen—turned upwards in various directions; suddenly aware of the fish, or of its shadow, it quickly draws up its whole body, thus contracting the glands in the skin on all sides with considerable force. Granting that this force is sufficient to express the globules of secretion from the pores of the glands, these, as the skin contracts, must inevitably be expelled from them; instead of flowing over the skin of the creature's back, they will be shot into the air in hundreds —or thousands—towards the pursuing fish; the fish, now alarmed on its part, and hit by the shower of minute shot, which may be in some way injurious or offensive, retires from the pursuit, and the Onchidium is safe.

Of course, as I have already said, this is merely an hypothesis; the question nevertheless arises whether it may not be possible to show by indirect evidence that it is extremely probable.

It would, no doubt, be quite conceivable that the Onchidium might be able to defend itself in the mode I have suggested, not merely against the Periophthalmus and Boleophthalmus, but against other foes. But if, as I believe, these two fishes are actually the only, or at any rate the most dangerous, enemies it has to dread, and if the eyes and glands thus serve as weapons of defence against these fishes only, we must expect that wherever these fishes occur Onchidia with dorsal eyes will be found. This is in fact the case. The Periophthalmus is

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found in North Australia and the western portion of the Pacific, in the whole of the Chinese Seas as far as Japan, in the Indian Ocean and the Malayan Archipelago, and on the east coast of Africa. The Onchidia with dorsal eyes have precisely the same distribution.

Only one exception existed until lately. On the coast of Congo, where, from Günther's catalogue of recent fishes, Periophthalmus has long been known to exist, no Onchidium had been found, and even in the latest list of African land-mollusca, which we owe to the industry of Martens, no Onchidium is included. However, in answer to an inquiry from me, I was informed by that admirable malacologist that he was in possession of several species which had lately been brought back from Congo by the German expedition to that coast. He was good enough to send me a specimen to examine; but unfortunately it reached me in so bad a condition that it was impossible to arrive at any positive conclusion with regard to the presence or absence of dorsal eyes.

It therefore is possible that the Onchidium found on the West African coast may not have such eyes, and thereby a strong argument would be raised against the hypothesis I have put forward. For, according to that view, we should be inclined to regard the dorsal eyes as an organ indispensable to the genus, since by them only could its extirpation by the fish be prevented. However, there are spots where the fishes which we regard as the chief enemies of the Onchidium do not live, and where nevertheless the molluscs occur and are by no means rare. One species, long since described by Cuvier as *Onchidium celticum*, is found on the Atlantic shore of England and France; another occurs in America, on the high northern coast; others again live on the west coast of both North and South America; the Galapagos Islands have their peculiar species, and in the eastern parts of the Pacific, as in New Zealand and Australia, many species are found. In all these places the fishes are absent, and all the species of Onchidium here mentioned—almost all of which I have examined anatomically—are devoid of dorsal eyes, and at the same time of the glands which, acting as weapons, can alone serve to demonstrate the use of the dorsal

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eyes themselves. Here, where the molluscs seem to be exempt from pursuit, the eyes and the weapon would alike be useless, and it is quite intelligible that they should not be developed on the back in these species. It is easy too to understand that they must have degenerated if ancestral Onchidia provided with eyes migrated to these regions, where, in consequence of the absence of the fishes, both the organs for defence and those for warning immediately ceased to be of use. In this way the absence of dorsal eyes in the species living in localities where there were no hostile fishes would seem to be a confirmation of the view suggested: That the eyes of those species furnished with them are of use in the way above described. One single difficulty, however, remains; the West African Onchidia perhaps have no dorsal eyes, and one single species living in the Western Pacific certainly nas none, though it lives associated with those fishes, the hereditary foes of its race. But even this exception may easily be explained by a somewhat closer consideration of the structure of the genus, and of the mode of development of the dorsal eyes.

In a former chapter I have already pointed out that every living cell or group of cells must possess every attribute of living protoplasm; they must be able to move or change their form; they must be capable of assimilation, reproduction, respiration, and secretion, and finally they must be capable of elaborating external impressions, and, if I may say so, of transmitting them to their consciousness. We know, moreover, that a lens has the property of collecting in a focus the different rays which combine to make white light, and hence it follows of course that in every papilla of an animal's skin, that is either spherical or formed on any other regular curve, a similar convergence of the rays falling upon it must ensue if these portions of the skin are only sufficiently smooth and transparent. The chemical rays or heat-rays which are thus concentrated by the papilla on any point lying within the skin, must be able to act upon some of the cells they impinge upon differently to others, since the reaction of two contiguous cells must always be slightly different. Thus certain cells will be particularly stimulated to an increased exertion of the secretive action which is

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common to them all, and these will become gland-cells; while others will not be stimulated at all, or be modified in some other way. Now, supposing that the cells, as yet unmodified, and lying in the focus of the lens or the papilla, were to come into contact with a sensory nerve, they might easily be converted into true sense-organ-cells, since they, as living cells, possess the inherent capacity of reacting on external impressions in the way to which we give the name of sensation; in the first instance, no doubt, these sense-cells could only transmit general sensations, and in this respect would at most be distinguished above the other contiguous cells by possessing that general sensibility in a somewhat higher degree. If now, in consequence of any influence, the cells of the epidermis subjacent to the lenticular prominence became surrounded with pigment, so that the rays concentrated by the lens could penetrate no deeper, it would seem that the first impetus would be given towards the development of a true eye. It may be assumed that this primitive eye would in the first instance only be capable of distinguishing different shades of light and darkness—a full light from a shadow. From this, by itself alone, the animal would derive no advantage, since this eye, though sensible of the shadow of a pursuing fish, would only give warning of the danger. But the same cause which originated the eye—*i.e.* the regular convex curving of the prominent part of the skin—will also have been capable of modifying some of the cells of that primitive cellular mass into gland-cells, and thus a weapon will have been formed. Not till then could Natural Selection step in with its stabilitating and extending influence, and develope from this simple eye, capable only of distinguishing light and shade, a perfected organ qualified to give an exact image of the fish in pursuit; and the glands when necessary, in the same way could become more effective weapons than they were at their first origin.

A pretty theory! may perhaps be said—but unfortunately merely an hypothesis. Granted. Nevertheless, I was able, in the course of my investigations of the development of the dorsal eyes as it takes place in nature, actually to observe all the stages, just as I have here deduced them from an hypothetical

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construction of the possible process of development of such an eye from the simplest conditions. A short account of these observations will here be of service.

All the species of Onchidium observed by me, the blind as

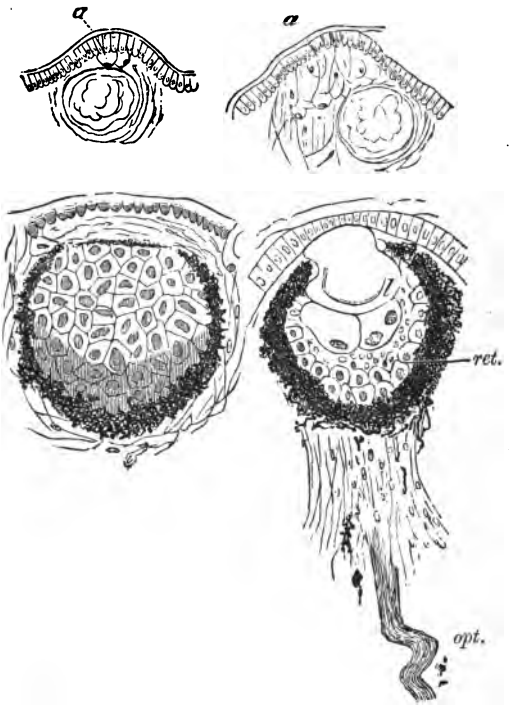

FIG. 101.—The development of the eye of *Onchidium*. Above, to the left, the first stage; small vesicular cells (*a*) close under the epidermis cells of the prominent point of the papilla. Above (right) a larger mass of these vesicular cells, which gradually increases and grows spherical. Below (left), this body of homogeneous cells is enclosed in pigment layer. Below (right), the eyeball thus formed communicates with the optic nerve (*opt*), and its cellular mass has been differentiated into a large lens lying in front, and retina-cells behind it.

well as those that can see, are covered with a great number of tubercles of various sizes, of which the surface is everywhere curved very regularly and is at the same time quite smooth. The intervening portions of the skin of the back are, on the contrary, distinguished by much roughness and granulation or

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wrinkling; hence in these intermediate spaces no uniform refraction of rays of light can take place in any one point, while it can in the smooth rounded papillæ. These vary greatly in size, and they constantly increase in number with the age of the animal. The smallest have beneath the cuticle, or outer skin, merely a simple cellular layer—the epithelium—like all univalves. The next in size show, exactly in the centre of the papillæ, a cellular mass growing inwards and downwards from the epidermis (see fig. 101, the upper fig. to the left), in which one or two cells may already be discerned as the basis of future gland-cells; in the next this group of gland-cells are pushed aside by another cellular mass proceeding in the same way from the epidermis at the summit of the papilla (see fig. 101, right, top fig.) and of peculiar aspect. Subsequently the innermost cells of this last-named mass become conspicuously modified, they increase much in size, their contents become peculiarly granular, and their circumference highly refractive, and then a fine nerve may be seen proceeding from the interior of the skin towards this cellular mass. In still larger papillæ we find roundish cell-bodies which are in direct communication with a nerve, and which at the back are already partly surrounded by pigment (see fig. 101, bottom, left fig.). At the spot where the nerve enters, and where the pigment layer is not altogether closed up, there are a few peculiar cells which are of precisely the same size and aspect as the cells above mentioned in the largest papillæ without pigment. Finally, the pigment layer closes round the central cellular mass, and the primitive rudimentary eye is complete.

The structure is not, of course, thereby definitely completed. Very striking modifications now take place in the central bodies, composed of homogeneous cells and enclosed in pigment; one of them, lying nearest to the prominent surface of the papilla—the cornea—grows more than its neighbours; soon others do the same, and a true lens, consisting of at least four cells, is thus formed. The still unmodified cells, lying between the lens thus formed and the pigment sheath, now are transformed into a retina of which the structure has been above described. The process and conditions here described, and con-

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firmed by actual observation of the development of one of the most highly developed dorsal eyes of the Onchidium, coincide—as I think must be allowed—with the phases of development previously set forth on hypothetical grounds as being those proper to the formation of an eye, if we assume that by the simple property of a regularly curved and smooth surface of a papilla of the skin, all the light, heat, and chemical rays of a beam of light must be made to converge in one point.

If the foregoing chain of argument is correct, as I cannot doubt, we have here detected an organ of extremely complicated structure in the very process of formation; and this instance proves, if indeed further proof were needed, that, as Darwin has often insisted, an organ can never be *created* by natural selection, but can only be modified and improved by it. Sometimes, no doubt, expressions are used, even by naturalists, which might lead us to suppose that they were of opinion that an organ might originate from its use—thus, in this case, an eye from the act of sight; this, of course, is absolutely erroneous. Sight, on the contrary, cannot occur till from other causes—as in this instance the direct stimulus to the skin—those parts have been formed which must be in existence before sight is in any way possible. Here, in the dorsal eyes of Onchidium, in the first instance it was the concentration of light on a certain point within the skin, which was occasioned by the form and structure of the papillæ, and the consequent modification of certain cells, which gave rise to a primitive organ of sight, and this organ was capable of still further development through natural selection, since, from the very first, it contained within itself the elements of further perfectibility and modification.

It follows, moreover, that if at any time such a primitive eye were developed in an animal which was not exposed to this process of natural selection by its association with a fish that preyed upon it, the organ, being useless, would disappear or at any rate degenerate. And this actually is the case, as we have seen; for all the species of this genus which live where the Periophthalmus does not, are devoid of these eyes. Only one ascertained exception is as yet known—the above-mentioned species of Onchidium which lives associated with species that can see

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and with the preying fish, though it is itself blind. But this species is found exclusively on the outer limits of the region inhabited by Periophthalmus, namely, on the south-east coast of Australia and in the central region of the Pacific. Also the species spoken of as living on the West coast of Africa, and which is probably blind, belongs to such another frontier district. Now it is, of course, not much to be wondered at, that in these frontier districts a blind form should occur among those that can see. But there is a much more striking argument for allowing this exception again to serve as confirming the rule. While all the truly blind species of those regions whence Periophthalmus is absent, are devoid, not merely of developed eyes, but of the first elements for forming them, and of the accompanying weapons—having no dorsal glands whatever, since without these the eyes would be useless—the blind species of the Pacific has both the glands and the cell-groups inside the papillæ agreeing precisely in structure with a middle stage in the series exhibited in the formation of the very highly developed eyes of *Onchidium verruculatum*. Thus here we seem to have a species in which either eyes formerly existing have begun to disappear from desuetude, or the construction of a true organ of sight has been begun by the coincidence of the three factors which would give rise to it.[124]

I have treated of this example somewhat in detail, on purpose to define as clearly as possible the limit-line where the external modifying causes which we discern as giving rise to a new organ—or rather as transforming one already existing into another—cease to be effective, and where those selective influences begin to act which determine the further perfecting of a newly developed organ.

I am, moreover, convinced that in every case, by a corresponding method of research, the same limit-line will be easily detected. That it is not yet recognised, nor even in most cases supposed to exist—so that it is often difficult to avoid a confusion between the transforming causes and the purely selective ones—is, in my opinion, entirely due to our having hitherto been satisfied with mere general speculations on Darwin's theory, and having neglected to investigate the innumerable problems

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which it suggests, but which can only be solved by experiment. I shall here discuss another important instance of the same kind which is very much to the point—the Means of Protection, namely, bestowed by nature on both pursuers and pursued to enable them to attain their end, that is to say to capture their prey on the one hand, or to escape capture on the other.

Protection by imitation of surrounding objects.—It is well known that a great number of living animals are enabled to escape their pursuers by their more or less strong resemblance in form and colour to the objects among which they live, in which case the resemblance is protective; while others, on the contrary, are specially qualified by the same circumstance to pursue their prey with success. Thus a crowd of new agents of selection among forms are added to those already discussed in the former chapters. For it is self-evident that every alteration that takes place in the co-ordination of the conditions which surround any given species of animal must deprive it of the protection it derives from its resemblance to a particular plant, let us say, if that very plant is exterminated; and in the same way that an accident of colouring, which has hitherto occasioned no special resemblance to any object, may suddenly become a powerful instrument in facilitating attack or self-defence. Thus a selection will be effected between different forms which had previously been equally protected.[125]

It is, of course, impossible to investigate in this place the greater number of the known cases of such protective resemblance, and it will suffice to discuss a few of the most instructive examples. I shall here adopt the arbitrary division of these cases into two classes, which has become general: into those, namely, of the resemblance of animals to inanimate objects—as stones, sand, the soil, and living plants—and those of resemblance to other living animals; but merely for convenience sake, since I can find no principle on which such an artificial division can be based.

It has long been a well-established fact that very many animals are effectually protected against their enemies by their resemblance to stones or sand, lichens, leaves and twigs; and every one who has at any time been engaged in collecting

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insects is familiar with numerous instances of this kind. Many birds and quadrupeds that are regularly hunted by men have become extremely rare in many places, because, though they are to a great degree protected against their enemies among other animals, by the resemblance of the colours of their feathers or

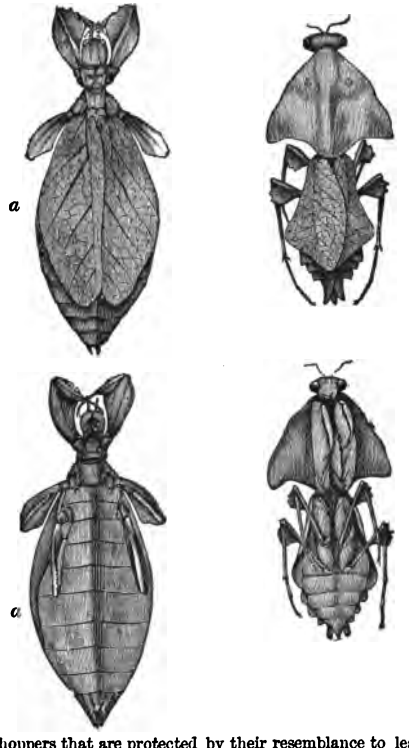

FIG. 102.—Grasshoppers that are protected by their resemblance to leaves. *a*, ***Phyllium siccifolium***, feeds on leaves and mimics fresh leaves. *b*, *Acanthops* sp., one of the *Mantidæ*, feeding on creatures which it captures among dry vegetable matter; it exactly mimics dry leaves. From the Philippines. Half natural size.

fur to the objects among which they live, man can employ a variety of means of attack or pursuit against which the protection of resemblance is ineffectual. The zoologist who should attempt to capture the perfectly transparent creatures which swim at the surface of the sea without using a net for straining

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the water, would certainly catch but a very few individuals with a glass vessel, for only under the most favourable circumstances would they be visible to him. A resemblance of colour to that of various parts of plants is in many cases increased in efficacy by the habit many creatures have of squatting close and motionless when they are pursued, so that their resemblance to a leaf or branch is greatly increased. The caterpillars of several species of butterflies are familiar to every one, as well as the 'dry leaf insect' (see fig. 102); this belongs to the class of leaf-eating grasshoppers, to which also belong the Phasmidæ, walking-stick insects (see fig. 32). They are perfectly harmless, and their resemblance to the objects which surround them is evidently only a means of escape from their pursuer. It is quite otherwise among the predatory Mantidæ, the best known of which is the 'praying mantis' (*Mantis religiosa*). In the accompanying cut I have represented a species of the genus *Acanthops* which has an extraordinary resemblance to dry leaves, but in this case the resemblance must be available in facilitating attack. Thus the same character may conduce to two different ends, attack or defence.

Besides the cases of protective resemblance in form and colour, which I have here briefly indicated, there are others which we might feel disposed to regard as the exaggeration of such a means of protection. In all the instances here mentioned the character of the form and colouring serves for purposes of concealment, irrespective of whether the ultimate end is offensive or defensive. But in many instances of brilliant and conspicuous colouring the case is quite otherwise, particularly among insects; their colours are so splendid, and the markings on the wings or body so striking, that they must inevitably attract the gaze of every insectivorous creature. Thus they would seem to be actually forced on the attention of their enemies, and it is probable that not one of these vividly painted forms could long escape annihilation if they had not some other means of protection; but this, in fact, seems to be invariably the case, as we learn from Wallace's admirable and exhaustive researches into this subject. Thus the gaudily striped bees and wasps have a sting connected with a poison-gland; other insects,

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as the stingless *Chrysididæ* and many proboscidian beetles, are protected by a strong coat of mail; bugs, lady-birds, and many butterflies have dermal glands from which the secretion—as every one knows in the case of the bug—is excessively objectionable to the pursuer, or even in some way injurious; others can escape pursuit by extreme rapidity of flight, while others again assume a peculiar posture by which—as it would seem—they can actually frighten away their enemies. It is in connection with these facts that, according to the statements of this distinguished naturalist and of other inquirers, such brilliantly coloured insects are usually, if not invariably, avoided by the generality of insect-eaters; birds—as well as frogs and lizards—showing a preference for the dull-coloured over the gaily coloured species. This view is strengthened by the fact adduced by Wallace that those insects or larvæ which are inconspicuous in colour are commonly devoid of any kind of defensive weapons such as are found in the more splendidly coloured species. Hence, according to Wallace, the use of the bright colours is evident; the creatures which pursue these insects soon learned by experience, and communicated to their progeny, the uselessness of pursuing these harlequin insects, as any attempt to attack them might be bitterly avenged.

At the first glance this view seems a striking one. It may be the correct one in many or all of the cases here adduced, but it is certainly open to doubt whether it can be unhesitatingly applied—as has sometimes been done—to every case of splendid colouring in the skin of animals. Darwin has already raised this question as against Wallace, and he proposes to substitute the view that all or most cases of brilliant colouring have originated from a variety of natural selection which he terms Sexual Selection. According to this view, colouring has resulted from the determining selective influence of the sexes and their preference for certain colours and modes of colouring. Still, Darwin himself had already mentioned, though only incidentally, that there are many animals characterised by their splendid motley or metallic colouring which could not have preserved it through sexual selection; for example, all the different Polypes, and more particularly the sea-anemones and

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true corals, are conspicuous for their colours. The surface of a reef lying just under water has often been compared to a gay garden of flowers, and the splendour of such a 'bed' of animals is in fact quite astonishing. It is as though Mother Nature had here given free play to the fancy she is elsewhere compelled to restrain in some degree, by indulging her delight in lavishing all the colours of the rainbow, and by inviting a motley company of creatures to disport themselves among the flowers and fruit of her submarine garden—blue and red star-fish, Holothuriæ of every hue, and gaudily painted fishes.

The fishes, in which the sexes are separate and which swim about freely, may perhaps have preserved their brilliant colouring by sexual selection, or even in the way put forward so emphatically by Wallace; but neither hypothesis suffices as a satisfactory explanation of the equally bright colours of polypes. No kind of sexual selection can here come into play, for the simple reason that the sexes do not seek each other; they are all sessile animals, male and female alike, and are obliged to throw off the sexual elements into the water and leave it to chance, or rather to the currents, whether fertilisation is effected or not. Wallace's explanation is equally inapplicable. All polypes are predatory creatures, feeding on fishes, crabs, worms, &c.; hence their striking and ornamental colouring would seem rather to be a disadvantage to them, for, since they cannot move about, they are fitted to catch such animals as approach too near to them with their long arms and the weapons with which these are furnished; and their colouring, therefore, would seem calculated to warn all creatures swimming in the sea, even at a distance, against coming within range of their perilous embrace. This apparent disadvantage might perhaps be outweighed by a greater advantage connected with this bright colouring, namely, that it warns the fish that prey upon them not to approach—which, of course, presupposes that those enemies have real cause to dread the weapons of the polypes. This, however, is by no means the case; the fishes which feed on the true corals—as the *Scaridæ* among the *Labridæ* (Wrasses) and the *Diodontidæ* among the *Plectognathi*—are perfectly indifferent as to whether the creatures they feed on try to clutch them with

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their tentacles or pierce their skin with their microscopic dart-like stinging-threads. It is impossible—so far as our present knowledge extends—to discover the faintest trace of usefulness in the brilliant colours of the polypes, and it is highly probable that they are in fact perfectly unimportant as regards the selective influence caused by their reciprocal relations with other animals. To this example of a mode of colouring which is insignificant with regard to selection, we might add many others, particularly of invertebrate animals; and the question even arises whether in many cases the distribution of colours, to which we are at present disposed to attribute a marked value in the process of selection, may not be considerably overrated in this respect.

But it follows from all this that not the colour or pigment itself merely, but its distribution—*i.e.* the markings of the animal—may under certain circumstances have been produced by other causes than those on whose effects selection seems to depend. It is perfectly evident that under no conceivable circumstances can the pigment, the colouring-matter itself, *originate* from selection; this point has already been gone into in Chapter III. (see pp. 99 and 115). It was there shown that the origin of the pigment must depend on physiological processes acting in the body of each individual, and which seem to be of the greatest importance to the healthy life of each. Hence the particular mode of its distribution throughout the skin must in the first place be the result of causes acting entirely in the animal itself, perfectly regular from the very first, or, it may be, wholly irregular; and this will depend on whether the internal physiological causes have determined the deposition of the colouring-matter in the skin in a certain regular order or no.[126] If this order is very sharply defined, the distribution of colour must, of course, be extremely regular, and many of the characteristic markings in Actiniæ, corals, and the shells of Mollusca may have arisen in this way. But, on the other hand, selection can control this colouring of the skin, and can confirm any particular arrangement which is especially advantageous to the creature in the struggle for existence, can make it more regular or enhance its brilliancy. The possibility that selection may

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control a mode of colouring that has originated by a physiological process, by no means proves that in every case without exception the distribution of colouring in the animal world must have originated in the same manner, any more than the established fact that chlorophyll is formed in most green-leaved plants under the influence of light, alters the other fact that in certain cases, as in the Coniferæ, the same matter can be elaborated in the dark.

A very striking instance of protective colouring is exhibited in the so-called Chromatic Function which has only recently been made the subject of exact investigation. It has already been discussed in the chapter on the influence of light (see p. 92 and note [27]). It consists in the power possessed by many Fishes, Crustaceans, Amphibia, and Reptiles, of adapting their general colouring—often by extremely rapid alternations—to the colouring of the surrounding objects, so that they seem to be helped by it in the pursuit of their prey, or especially protected against the attacks of their enemies.

Hence it is perfectly evident that all such adaptations of colouring to that of surrounding objects must be a powerful instrument of selection. Those individuals which are best qualified in this respect must have a conspicuous advantage over their less well-fitted companions in the struggle for existence. Thus every cause which might give a species the capability of rapidly assuming certain changes of the colour of the skin by a contraction of the chromatophores, would indirectly be the cause of a further perfecting of this capability by natural selection; but this selection could not come into play till the contractile power of the chromatophores was actually existent and a protective mode of colouring was already produced by it. Neither selection, nor the struggle for existence, could in this case, any more than in any other, by itself effect a modification of the functions or of the morphological peculiarities of an animal. And the same is evidently the case in those instances, now to be considered, of protective resemblance in form and colour which is commonly known by the name of *mimicry*.

The mimicry or imitation of one animal by another.—Bates and Wallace gave the name of *mimicry* to all those cases of

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protective resemblance in which a creature, otherwise defenceless, imitates the form and colouring of another which has some special means of protection, and thereby, as is probable, escapes the pursuit of its enemies more easily than it could without such a disguise. But here again the protection obtained may benefit the pursuer as well as the pursued; the former by disguising it in the eyes of the alert prey, the latter by protecting a defenceless animal which mixes with the better-armed species whose aspect it has borrowed. I need not insist once more that the words here used must be taken in a figurative sense, since it is clear that no animal can ever be capable of designedly *mimicking* another.

We owe the most important researches that have yet been made on this interesting subject to the above-mentioned judicious and acute travellers. No doubt we have long been acquainted with insects living here, in Europe, which in form, colour, and mode of flight bear a great resemblance to others of different species; I may mention the *Sesiæ* among the butterflies, which greatly resemble bees, and owe to this resemblance many of their specific names.[127] Formerly, little attention was paid to this circumstance; at most it was incidentally noted that those butterflies were apparently protected by this resemblance, but any attempt to explain this mimicry was never even thought of before Darwin and Wallace; and it was partly the new views which, from Darwin, rapidly extended among zoologists, and partly the vast number of striking examples of such resemblances in tropical Brazil, which led Bates in the first instance to examine the relations of these cases more exactly, during his many years' residence in South America.

A brief enumeration of the most important examples of such mimicry will here be desirable; but a complete list is all the less necessary because the labours of Wallace, Bates, and Trimen are easily accessible, and popular essays on the subject have appeared in many periodicals. Among the American butterflies the species of *Leptalis*, *Erycina*, and *Ithomia* mimic the *Heliconiadæ*, which are distinguished by a sharp and unpleasant smell. In the same way the *Danaidæ* and *Acræidæ* of the eastern regions of tropical America are protected by fœtid

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glands, and here again there are certain species of these families which are imitated by the defenceless species of *Papilio* and *Diadema*. In North America, *Danais archippus*, a very common butterfly, is closely copied by *Limenitis archippus*;

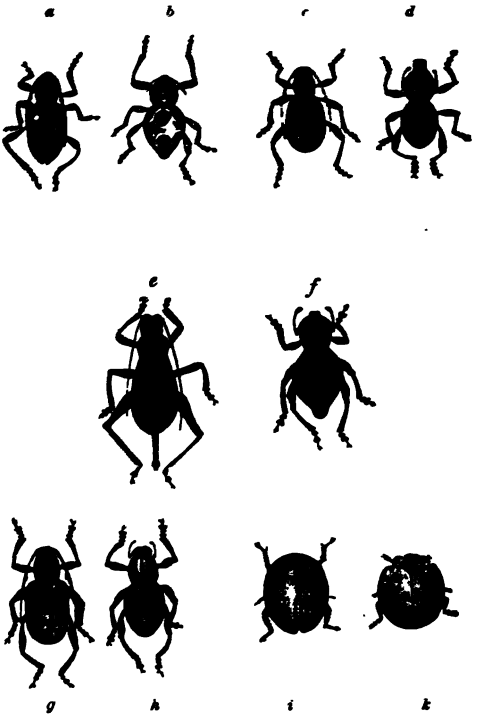

FIG. 103.—*a*, *Doliops* sp. mimics *b*, *Pachyrhynchus orbifer*; *c*, *Doliops curculionoides* mimics *d*, *Pachyrhynchus* sp.; *e*, *Scepastus pachyrhynchoides* (a grasshopper) mimics *f*, *Apocyrtus*; *g*, *Doliops* sp. mimics *h*, *Pachyrhynchus* sp.; *i*, *Phoraspis* sp. (a grasshopper) mimics *k*, a *Coccinella*. All from the Philippines, of nat. size. It is evident that the great similarity of the creatures to those they mimic is less conspicuous in the engraving than in real life, since the exact correspondence in the colouring cannot be given here.

species of *Sesia* and of *Ægeriidea* so closely resemble small wasps that every one fears to handle them, but they have no sting like wasps, and are in every respect perfectly harmless. Among beetles, the *Hispidæ* and *Eumorphidæ*, which are pro-

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tected by fœtid glands, are imitated by various species of stag-horn beetles; other tropical staghorn beetles look extremely like certain *Curculionidæ*—the *Pachyrhynchidæ* (see fig. 103)—which have an integument so hard that insect-eating birds avoid them, probably on that account; other beetles, as, for instance, *Charis melipona*, resemble true bees; *Odontocera odyneroides* resembles a wasp of the genus *Odynerus*; the grass-hopper *Condylodera tricondyloides* is wonderfully like a beetle, *Tricondyla* of the family of the *Cicindelæ*. Many flies are

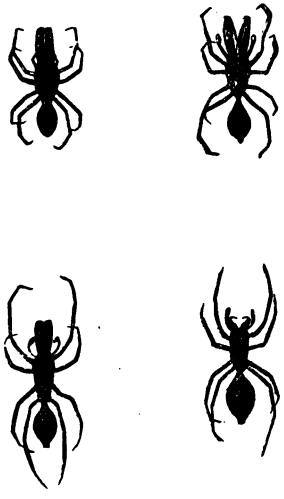

FIG. 104.—Spiders which mimic ants and live associated with them; it is very difficult to distinguish them.

very like wasps; spiders which live associated with ants have assumed the form and colour of the ants (see fig. 104), and Bates mentions a singular instance when a large caterpillar frightened him extremely by its extraordinary resemblance to a poisonous snake. Even among Vertebrata, such cases are not rare. Wallace tells us that several species of the poisonous genus *Elaps* (snakes that are common in Brazil) are closely imitated by quite harmless snakes—thus *Elaps fulvius* is copied by *Pliocerus æquilis*; a variety of *Elaps corallinus*—

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known as the coral snake—by *Homalocranium semicinctum*; *Elaps lemniscatus*, of which the bite is said to be absolutely fatal, by *Pliocerus elapoides*; and all again are imitated by various species of the quite harmless genus *Oxyrhopus*, which live associated with the poisonous kinds. The two cases, communicated by Wallace, of birds which mimic other birds, seem certainly to come under this head; the *Tropidorhynchus*, dreaded for its strength, is mimicked by the helpless *Mimeta*, and *Accipiter galeatus*, a bird of prey which feeds on other birds, exactly resembles the insectivorous vulture *Harpagos*, wherever the two species occur together. But the only instance adduced by Wallace of mimicry among quadrupeds—the resemblance of an insectivorous *Cladobates* to the squirrels (rodents)—seems to me, on the other hand, to be included with less reason in this class of resemblances. The assumption seems to me without foundation that the squirrels are harmless creatures and cannot alarm the insects around them by their movements, so that the Insectivora which resemble them easily capture their food. The European squirrel, at any rate, is omnivorous, as are many rodents; and granting even that they never eat insects, it does not appear to me to be by any means established by observation that insects would remain motionless when the squirrel, as he leaps from bough to bough, shakes every leaf and twig.

Thus, omitting this case of the imitation of a squirrel by an insectivorous animal, the cases of mimicry that are here mentioned seem to be well established on the whole. In each case it can be shown that the mimicked species is in some way very effectually protected by an offensive smell, weapons of some kind, a hard skin, a powerful frame, &c., while the mimicking form is, without exception, weak and devoid of defence, so as to be greatly in need of protection. It can, moreover, be proved that in many cases, if not in all, the mimicking species live associated with those they resemble.

From the facts thus established by observation, Bates and Wallace argue as follows. They show that all mimicking forms have acquired, by their disguise, an undeniable advantage in the struggle for existence over those less well equipped, since, in consequence of the disguise, either they escape

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notice by the animals they pursue, or they are no longer liable to pursuit, because the predatory species to which they might perhaps afford a dainty morsel regard them as being—like the creatures they resemble—bad eating or even injurious. In this case the prey deceives the pursuer; in the former case, on the contrary, the pursuer deceives the prey. The mode of origin of this wonderfully strong protective resemblance can be explained by the well-known principles of selection; protective resemblances, at first small, have been developed by elimination to a greater, and at last to a perfect pitch of mimicry in form and colour, and also in mode of life. This theory seems extremely plausible, and I believe that in many cases it is the right one; whether it is in all is another question. Under no circumstances can this theory account for the first appearance of the resemblance, as seems to be tacitly assumed by many writers. But before I enter on any further discussion of this point, I will describe a few new cases of mimicry observed by myself.

True cases of mimicry among Mollusca have not yet—so far as I know—been observed, although instances of protective resemblance are not rare even among them. This is surprising, since we might suppose that mimicry might originate where a protective resemblance to inanimate objects or plants already existed, for there seems to be an *a priori* probability that mimicry may have been developed from this. Perhaps this and other gaps result from our very meagre knowledge of the habits of life of the animals, particularly the invertebrate animals, of other countries.

Before describing the cases observed by me of mimicry among land mollusca, however, I must make a few remarks on the system of classification of land mollusca now in vogue. The system according to which they are classified is based almost exclusively on the practical requirements of the collector, *i.e.* on the comparison of the empty shells; on the other hand, the investigation of the animals themselves has until quite recently been very much neglected. But the anatomical researches carried on during the last ten years—to which I believe I have contributed a no inconsiderable share—prove that the shells of such

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land-snails as have, like the great vine snail (*Helix pomatia*), a wide mouth to their shells are extraordinarily variable. Genera which had been constituted merely on our knowledge of these variable shells, such as *Helix*, *Bulimus*, *Vitrina*, *Nanina*, &c., have proved quite untenable, and we now know that species which, by a comparison of the animals, must be placed actually in different families, often have shells so exactly alike that conchologists and palæontologists—the latter having, of course, nothing but the shells to judge from—have placed them in the same genus.

These recent investigations have, moreover, proved that the great majority of the genera of land mollusca have very narrow limits of distribution, so that with regard, for instance, to the numerous shells resembling Vitrina which have hitherto been described, their local origin supplies a far surer index as to their affinities of relationship to this or that genus than the characters of the shell itself. Setting aside a small number of cosmopolitan and for the most part minute forms, most of them, and particularly the larger kinds, are highly characteristic of the different countries where they are indigenous. Thus the three genera, *Cochlostyla*, *Helicarion*, and *Rhysota*, are quite characteristic of the Philippines; for only a few of the species extend into the neighbouring islands of the Moluccas, while they occur in a very great variety of differently characterised species in the Philippines themselves. Pfeiffer, who as a conchologist was beyond a doubt the highest authority, included the species of Cochlostyla in three different genera, and those of Helicarion in two; but anatomical investigation has proved to me that the species of these three genera, in spite of the great diversity of their shells, are quite as much alike as the different races of the Germanic or Romance nationality.

The species of these three characteristically Philippine genera are mimicked in a very remarkable manner, both in form and colour, by species of other genera which are not characteristic of the Philippines only, but of the neighbouring groups of islands as well; one of these cases is, beyond a doubt, one of the most striking instances of true mimicry.

The animals of the species of *Helicarion* (see fig. 105, *c*)—of

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which the nearest allies are found in Australia and the islands of the Pacific—are easily recognisable at the first glance by the mantle lobes, which cover the thin transparent shell, and by their remarkably long, narrow, high-ridged tail, which ends abruptly in a gland; a kind of horn, sometimes of some length, projects from the tip of the tail. The numerous species—of which the various distinguishing characteristics are much more conspicuous in anatomical details than in the shell—live on trees in damp woods, often in great multitudes; they are very active and creep about with considerable rapidity upon the twigs and leaves of

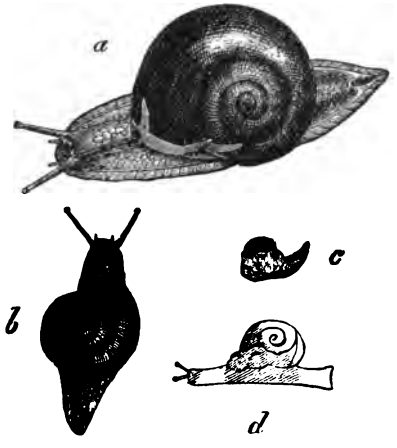

FIG. 105.—*a*, *Rhysota Antonii*, a land mollusc of the Philippines, mimicked by *b*, *Xesta mindanaensis*, which lives associated with it; *c*, *Helicarion tigrinus*, mimicked by *Xesta Cumingii* from the same locality. Half nat. size.

the trees. Every species that I personally examined possessed the singular property, which many lizards have—particularly the Geckoes—of shedding their tail when they are seized somewhat roughly, at a little way behind the shell. This they do by whisking the tail up and down with extraordinary rapidity, almost convulsively, till it drops off; if the creature is held by the tail, it immediately falls to the ground, where it easily hides among the leaves. If it is laid flat on the hand, the rapid wagging movement is strong enough to raise the body with a

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spring into the air, so that it falls over on to the ground. These snails at first constantly escaped me and my collectors in this way, and not unfrequently we had nothing but the tail left in our hand. According to Guilding's observations the same peculiarity of parting with the hinder prolongation of the foot characterises the West Indian snail *Stenopus*. I ascertained by further investigation that in a free state of nature such self-mutilation not unfrequently occurs, for out of about a hundred specimens of *Helicarion gutta*, which is extremely common in the north-east of Luzon, I found perhaps ten individuals that had shed their tails, or, to speak more accurately, the hinder end of the foot, and had the stumps partly healed, or the foot to some extent grown again. Now, this hinder portion of the foot is the most conspicuous part of the snail's body, and it may be supposed that it is, in most cases, the part first seized by the reptiles or birds that prey upon them; but, startled by the escape of the body itself, they would soon learn to recognise, by the form of the tail, those species which were capable, by this self-amputation, of depriving them of the larger and probably the only valuable portion of the prey. In this way the species of the genus Helicarion can escape the pursuit of their enemies better than they otherwise could on account of their exposed mode of life, and it is in agreement with this fact that, in the spots where they occur, they are commonly to be found in numbers together. But other land-snails which are not in fact protected by any such peculiarity might very well be equally effectually protected by mimicry of the appearance of a Helicarion, since they might thus be mistaken for them.

One single species of snail does, in fact, exist in the Philippines which actually bears an extraordinary resemblance to the species of Helicarion, although in internal structure it is, systematically speaking, very far removed from it, and does not even belong to any of the genera which are characteristic of these islands; this is *Vitrina Cumingii*, a species long since known as having been discovered by Cuming in Mindanao (see fig. 105, *d*). An examination of the living animal convinced me that it belonged neither to Vitrina nor to Helicarion, but to a thoroughly Indian genus, *Xesta*, of which the very numerous

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species which live in the islands of the Malayan archipelago are distinguished by their very thick and brilliantly coloured shells. *Xesta Cumingii* has, on the contrary, a thin transparent shell, which during life is covered by the lobes of the mantle in the same way as the species of Helicarion; indeed, it is on the ground of the form and texture of the shell that it has hitherto been placed in the genus Vitrina. It has, moreover, the long foot which distinguishes Helicarion, and, in fact, I supposed this species to be one of that Philippine genus, until I had examined it anatomically, and so had convinced myself that it belonged to the Indian genus, though it has almost no external resemblance whatever to the other species. Thus *Xesta Cumingii* has assumed to a very great extent the appearance of a Helicarion; moreover, it lives, as I can aver from my own experience, in precisely the same spots as Helicarion, namely on the upper side of leaves in damp woods, and so mixed with that genus that it frequently happened that I captured a specimen of Xesta when I thought I had a species of Helicarion. But it does not possess the power of self amputation which is characteristic of that genus, and hence, when caught by the tail, by a snake or any other creature, it cannot escape in the same manner.

It follows from all this that we may assume on good grounds that we have here a case of true mimicry—at least it seems hardly possible to think that it is only a singular coincidence. Even Wallace's test and criterion of true mimicry is perfectly applicable here; while the model form (as we may call it) which has a real means of protection is extremely common, the imitating and defenceless form is found in solitary specimens. Hence, the question arises, whether, perhaps, there may not also be in the West Indies land mollusca mimicking the *Stenopus*—which is provided with the same means of protection as the species of Helicarion in the Philippines—so as to be protected in the same way as *Xesta Cumingii*. If this should prove to be the case, it would afford, as it seems to me, a strong argument for the accuracy of the view here put forward, that *Xesta Cumingii* is, in fact, effectually protected by the disguise it has assumed in imitating the species of Helicarion.[128]

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Moreover, there are very many instances of similarity of colouring between two creatures very remote from each other, and in which it is very difficult to discover any relations between the two animals thus characterised. Thus, many Annelida, Mollusca, Planariæ, and Ophiuridæ live on the stocks of the keratose corals, which they resemble greatly in colouring though not in form. In the same way all sorts of creatures may be found, on the disks of star-fish and Comatulæ or on the spherical shells of Echinidæ, which have perfectly assumed the colour of the animal on which they live. Here, certainly, we cannot speak of mimicry in the strict sense; it is far more probable that this resemblance serves only to enable these creatures to escape detection, living, as they do, exposed to a certain degree of danger on the surface of others. But, in the case I shall now describe, it appears to me that it can be of no use even in this way.

Together with *Xesta Cumingii* a second species of the same genus lives in Mindanao which differs quite as much from *Xesta Cumingii* as this species does from those inhabiting Java or the Moluccas. On the other hand, its shell looks exactly like those of the species of *Rhysota*, a genus in the highest degree characteristic of the Philippines (see fig. 105, *a*). These have shells of a uniform brown colour, often wrinkled and somewhat depressed, and not overlapped at all by any marginal development of the body—the lobes of the mantle. The foot is flat, broad and short, and bears at the end a gaping gland. All the species of Rhysota live on the ground under trees; and when, on particularly damp days, they quit the ground, they never climb trees, but only low plants growing in deep shade. It was from its sharing these characteristics that I regarded the new Xesta—which I called *Xesta mindanaensis*, from the locality where it exclusively occurs—as being a true Rhysota till I had the opportunity of examining it anatomically.

Xesta mindanaensis and *Xesta Cumingii* are the only two species of this Indian genus that are widely distributed in the Philippines; the latter is found from Mindanao as far as Bohol and the southern part of Leyte; the former occurs exclusively in Mindanao, the southern island. But while their nearest

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allies in Celebes, the Moluccas, Java, and elsewhere, exhibit all the typical Indian characters both of the shell and of the animal, both the species that have migrated into the Philippines are so completely metamorphosed as to the form and colour of both animal and shell that it would have been impossible to guess, without the closest anatomical investigation, that they did not belong to the genera proper to the Philippines. With regard to *Xesta Cumingii* the explanation is available that here we have a case of true protective mimicry; but how can we account for the even more striking resemblance between *Xesta mindanaensis* and a Rhysota? This resemblance cannot certainly be regarded as protective mimicry, since the species of Rhysota have absolutely no peculiar property by which they are better protected against their enemies than other mollusca, and consequently an imitation of their appearance can be no sort of advantage to the other imitative species.

The difficulty which is evident in the case just described is still further enhanced by the fact that other similar cases are known, and actually in the Philippines. By far the greater number of the brilliantly and variously coloured land-snails of these islands live on trees and belong to the highly characteristic genus *Cochlostyla*. The forms of their shells, too, are so extraordinarily various that they have hitherto been included in three or four genera (or sub-genera), and I am convinced that any palæontologist to whom the various species—above 200—should be submitted in a fossil state would distribute them into at least six, or more, genera. Anatomically, however, they are so nearly alike that it may be confidently asserted that there is no other genus of land mollusca at once so rich in species and so exclusively distinct as this of Cochlostyla; also, with the exception of six, or at most eight, forms, which occur on the small islands in the vicinity, they are confined to the Philippines.

With them, there occur there only two small groups of true Helicidæ; one of which, *Chlorœa*, lives on trees, while the other, *Dorcasia*, is found among grasses and low-growing plants, or even half buried in the soil. Neither genus includes many species, and the greater number of them occur in the northern

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part of the island of Luzon; not a single species of *Chloræa* is found in Mindanao, and only one of *Dorcasia*. Now, the anatomical investigation of several species of both groups (see fig. 73) has proved that they are very nearly allied to each other, and, at the same time, to one of our commonest European land-snails, *Helix fruticum*. But as regards their shells they differ so widely that in systematic classification *Chloræa* is placed far from *Dorcasia*, and also from *Fruticum*. The shell of *Dorcasia*, however, is easily recognised as allied to *Fruticum* from its resemblance to that type in colour, form, and marking, so that it is to me quite incomprehensible why conchologists should hitherto have disregarded so striking a similarity in the shells. On the other hand, all the shells of the group of *Chloræa* so singularly resemble those of Cochlostyla, of which the animals follow the same mode of life as the species of *Chloræa*, that they have hitherto been generally regarded as species of the Philippine genus, and in many of the species it is, in fact, quite impossible to decide which they belong to, so long as the shells alone are compared. Thus, on one side, a few species have preserved their resemblance to *Fruticum*, and with that the same mode of life; and on the other, a few have assumed the aspect of another genus and live on trees associated with certain species of it. Hence *Helix fruticum* ought properly to be included in one genus with *Chloræa* and *Dorcasia*, and thus combined they would be closely connected with the genus Cochlostyla. Supposing now that a form represented by *Helix fruticum* were the original form—as there are various reasons for supposing—some few species of that genus, when they migrated into the Philippines, would have preserved their original external appearance and at the same time their old habits of life; while others, acquiring the habit of climbing trees, would have become so much modified in form, colouring, and sculptured marking, that the closest scrutiny of the shells alone would not suffice to decide the question whether they belonged to Cochlostyla or not. We might then easily be tempted to attribute this similarity to a process of protective mimicry; but such an assumption would be at once contradicted by the fact that the species of *Chloræa* and *Cochlostyla* which most resemble each other, do

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not live associated together, and even for the most part occur on separate islands. Hence, it is impossible in this case that the resemblance should have originated by selection through mimicry, since protection by imitation against pursuit is here out of the question.

The question that then occurs is, how such a remarkable likeness in form and colour between two quite distinct creatures can have originated. I will investigate this problem by means of yet another example, because it is by this means that we may most easily succeed in ascribing to the influence of mimicry its due proportions, and in showing that this branch of natural selection, like every other, can do no more than avail itself of such characters as already exist for its own purposes—so to speak—but can never be in a position to act as a funda-

FIG. 106.—*Myxicola infundibulum*, copied from Claparède.

mental cause, originating differentiation in the form and colour of animals.

During my last stay at Port Mahon in the Balearic Islands, I found among the polypes of *Cladocora cæspitosa*—a coral which is there very common—a species, as it seems to me new, of the genus Myxicola (Annelida). I have here given a reproduction of Claparède's representation of another species of this genus (fig. 106). The species of this genus spread out the tentacles with which the head is furnished—and which are often regarded as branchiæ—in the form of a funnel; the sides of this funnel are perfectly closed and are formed of the filaments of the branchiæ which lie in the closest contiguity; the section of the funnel is circular. Each branchial filament has on its inner surface a multitude of fine and minute hairs, which, however, are rendered rigid by having in their interior cartilaginous cells; these hairs radiate towards the centre of the funnel, so

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that the space enclosed within the funnel is divided perpendicularly by a great number of septa into a corresponding number of chambers.

The new Myxicola cf Port Mahon I found, as I have said, among the polyps of Cladocora; they lived in long mucilaginous tubes which they had formed in the rifts in the coral, and in which they could move about freely. As long as no light was thrown upon them they protruded themselves just so far as that the top rim of the corona of tentacles was on a level with the tentacles of the polyps, so that when the worm and the polyps were both extended the coral itself presented a perfectly level surface of cups. Moreover, the funnels of the Myxicola were of precisely the same chocolate-brown colour as the polyps; and when fully extended the interior of the funnel formed by the tentacles looked exactly like the oral disc of one of the neighbouring polyps, for the radial pinnules were in the same position as those lines which, on the oral disc of the polyp, radiate towards the narrow central oral slit; in the Myxicola also a small central slit was observable, and all the parts which corresponded so exactly in size and position also displayed exactly the same colouring of greenish-grey with radial lines of a lighter hue and a narrow white streak in the middle. In short, the resemblance, in size, position, and colouring, of every part of the two creatures was so perfect that for a long time I took the corona of the Annelid for a polyp, until by an accidental blow I caused all the Myxicolæ of a large coral-stock to shrink suddenly into their tubes, though it was not severe enough to induce an equally rapid movement in the polyps of the apathetic Cladocora. At the first moment I must confess I felt an almost childish delight at having detected so flagrant an instance of protective mimicry: here was a defenceless tube-worm evidently most effectually protected by its resemblance to a polyp well defended by powerful weapons.

However, I soon found reason to doubt this interpretation of the facts; why should the Annelid require any such protection, since it could withdraw itself with the swiftness of lightning into its tube imbedded in coral, where probably no enemy would be able to follow it? Still, the wonderfully complete

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resemblance between the two creatures could not be disputed, nor could the fact that this resemblance was perfectly normal. Among the hundreds of specimens of Myxicola which I found in various pieces of coral, procured from the most various localities, I never found one that had not these same points of resemblance to the polyps. One day, finally, I found a marine sponge in which hundreds of this same Myxicola were living, and in every portion of it their funnels of tentacles extended just to the level of the surface of the sponge; but the sponge was coloured very differently from the Annelida, so that these when protruded were very easy to distinguish from the sponge. I then sought for the Myxicola in other spots, and succeeded in finding it almost everywhere; in the rifts in rocks and in the sand, between marine plants or the tubes of other worms—in short everywhere—and wherever I examined it closely it was exactly of the size and colour of the polyps of *Cladocora cæspitosa*. Mimicry, it is plain, is out of the question; the resemblance between the two creatures is simply and wholly accidental.

It seems to me that the obvious conclusion from all this is that, under some circumstances, the most perfect and complete resemblance between two creatures not living associated, may originate without its being referable to the selective power of mimicry, *i.e.* a protective resemblance. The possibility might certainly, however, be conceivable that that resemblance may originally have been acquired by such means, and subsequently retained after the Myxicola had been enabled, by the aid of some other means of protection, to establish itself in various other places. We have not, however, any single analogous instance to support this assumption; besides, it should be observed that all the species, without exception, of the genus Myxicola have the same funnel-shaped arrangement of their tentacles, and the colouring of their head generally harmonises with that of many polyps; they are commonly brownish, greenish, or red. A general resemblance between the worm and the polyps is thus of common occurrence; and as we are compelled to assume other causes than selection by protective resemblance in explanation of this likeness, it will be equally

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easy to deduce from analogous causes the somewhat more perfect likeness in form and colour between Cladocora and the undescribed Myxicola.

Still, true mimicry might, no doubt, be developed from such a case of extreme resemblance between two quite distinct creatures. Supposing that some animal not hitherto living in the sea at Port Mahon were to be introduced there which was able to capture the Annelida wherever their unlikeness to the objects around them—as the sand, sponge, &c.—rendered them conspicuous, they would only find the protection they would need by living associated with the coral, because there only could they be effectually concealed. And if the enemy—pursuing them even among the polyps of the Cladocora—should have learned to regard the polyps as dangerous foes whose fine stinging threads were capable of inflicting much injury, a perfectly characterised case of true mimicry might be developed from this instance, originating in simple shelter.

The theoretical possibility of the process thus indicated cannot, I think, be denied; but then the question arises whether many cases of mode of colouring and resemblance which we have hitherto been disposed to regard as cases of exquisite mimicry may not have originated in the same way as the spurious mimicry of the Myxicola. And here we find ourselves brought face to face with the same conclusion that we have become familiar with in each separate chapter of this work, and which I must once more repeat: Namely, that no power which is able to act only as a selective, and not as a transforming influence can ever be exclusively put forward as the proper efficient cause—*causa efficiens*—of any phenomenon. In all cases, including those of mimicry, the point finally must be to investigate the causes which may have availed to produce, by their direct action, any advantageous and protective change of colouring; it was not until the change had actually taken place that selection between the better or worse endowed individuals could lead to the further development of the advantageous character. It is extremely difficult to decide in particular cases—in most, indeed, it is impossible—the precise point where one ceases and the other begins to act. But it is precisely by reason of the

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universal difficulty of deciding whether a certain modification which has taken place is to be ascribed to some direct determining and transforming cause, or to the enhancing of a previously modified character, which is frequently connected with selection, that it becomes imperative that we should in the first place carry out the most exact research possible by means of experiment, and also wean ourselves of the convenient—but, as it seems to me, highly pernicious—habit of theoretical explanations from general propositions. Otherwise there is great danger that the bright expectation which Darwin has opened out to us by his theory may be baffled—the prospect of gradually bringing even Organic Being within reach of that method of inquiry which seeks to discern mechanical efficient causes.

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NOTES

INTRODUCTION

Note 1, *page* 10. Professor Marsh has lately discovered a colossal fossil reptile, belonging to the family of the Atlantosauridæ, and which was of such enormous size—more than eighty feet long—that it could hardly have been able to drag itself along on the ground or even to raise itself, if its bones had been as heavy in proportion as those of the reptiles or mammals now extant. And in fact the bones of this fossil Saurian are remarkably light in comparison with their size, so that Professor Marsh's view that the peculiar large cavities which occur in all the bones of the skeleton were air-cavities, and that they were thus actually pneumatic bones, seems highly plausible.

Note 2, *page* 17. There must, of course, be a number of characters of adaptation, of which we cannot avail ourselves as hereditary characters of general importance, from their appearing only in small groups, or merely in genera and species, or even in single individuals; these lose all diagnostic value in an inquiry as to the relations of affinity among the larger categories to which the animals under comparison may belong. Hence arises the necessity, insisted on in the text, for inquiring how far hereditary characters of general value are to be distinguished from characters of adaptation. But every character which can be regarded as a true sign of the common descent of large groups of animal forms, may be ultimately traced to the stage at which it first appeared, and where it was a character of adaptation. An example will help to explain this. We know that in all the Vertebrata, without exception, the first appearance of the skeleton, which is the most important organic system of the vertebrata, is inseparable from the presence of an axial cord, known as the notochord, or *chorda dorsalis*. This does not become merged in the vertebral column, but is displaced by it; it is perfectly inarticulated—a simple string of cells. The great uniformity of the conditions of its first appearance, structure, and position

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in the embryo of every vertebrate animal, show that we here have to deal with an hereditary character, and its remarkable persistence and constancy are evidently due to the fact that its presence is essentially bound up with the development of an organ so wonderfully fitted for the most various morphological and physiological differentiation as the vertebral column (and skeleton) of the Vertebrata. But, working backwards, in the series of invertebrate animals we first lose sight of the skeleton, and presently even the *chorda dorsalis* disappears.

From this it would seem that such an axial cord must have appeared at first, once or even more than once, in some group of invertebrate animals, *i.e.*, was elaborated from cells already existing in other forms. This primitive chorda must from our point of view have had some definite function, and from everything that we know of the histology of the cells of the chorda, we must regard it, even in its simplest form, as an elastic prop or fulcrum for the movements of the animal; consequently the primitive chorda was an organ that derived its fitness to exist from its adaptation (and consequent modification) to the function of affording support to the whole animal structure. Thus in the first instance it can only have had the value of a character of adaptation. Moreover, it must inevitably have preserved this value only, if it had not contained, in itself, and through its influence on the other organs connected with it, the elements of the most varied differentiation into numerous dissimilar forms. It is only by the fact that it and the tissues immediately surrounding it were in the highest degree plastic, that it acquired its value as an hereditary character. An accurate analysis of each separate organ will bring us ultimately to a stage in which its existence seems to be wholly dependent on its special adaptation to some definite purpose, or to some condition of existence.

Note 3, *page* 17. Rudimentary organs are extraordinarily numerous, and occur in a more or less significant form in most animals. Their high theoretical importance has been sufficiently indicated by Darwin, to whose works the reader is referred. Their most essential peculiarity is their incapacity for fulfilling the functions for which, by their structure and position, they would seem exclusively intended. The question, however, still remains, as Leuckart has pointed out, as to whether we are justified in saying that such rudimentary organs are in fact wholly useless. The teeth of the Vertebrata are, as we know, used only for biting and masticating, or as weapons. The male dugong does, in fact, so use his tusks, as is shown by the invariably worn condition of the point, on the external surface of each. The female has equally large, nay, even larger tusks; but they are not used—at any rate, not in the same way. But it seems not improbable that, merely by their great weight, they may assist in certain movements of the head, for instance, in grazing on sea-weeds; and in this respect they may actually have acquired a physiological significance without losing their character as rudimentary

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teeth. The most extreme case in the whole series of rudimentary organs which have lost their original use is offered by the roots of the Rhizocephala (*Peltogaster*), (fig. 12, *a*, p. 47); the parasite plunges them into the body cavity of the host it lives upon, and absorbs its nourishment through them. When the parasite has reached a certain age, it falls off, leaving its roots in the body of its host; they live on, though their purpose as organs of nutrition for the *Peltogaster* is, of course, entirely lost.

Note 4, *page* 22. This use of the clinging foot of the Geckotidæ is well known. In handbooks of Zoology—even in Claus—we read that these clinging hairs or suckers are formed by the secretion of a glutinous matter from the glands of the toes. I do not know on what this assertion rests, but there is, in fact, no truth in it. In the first place, there certainly are no glands present on the feet and toes; the clinging power is, on the contrary, effected in a wholly mechanical way, and derived from the rows of bristles beneath the toes, resembling the sucking discs of flies or of leeches. By the pressure of the foot on a smooth wall, the air between it and the wall is quite driven out; when the pressure is removed, the inner surface of the foot is raised by the elasticity and rigidity of the hairs, and this effect is increased by the special muscles which move the lobes, each of which bears bristles; thus a vacuum is formed between the wall and the sole of the foot, and atmospheric pressure secures the foothold.

CHAPTER I.

Note 5, *page* 27. Thacker has lately attempted to solve this problem on morphological grounds (Connecticut Academy, 1877, vol. iii., *On Median and Paired Fins, a Contribution to the History of Vertebrate Limbs*). He is of opinion that the four extremities of the vertebrata are to be considered as the survivals of two longitudinal folds of the skin, such as are to be seen in the living Amphioxus. If this attempt could be successfully followed up, we should no longer have to seek the analogues of the extremities of the Vertebrata among the Invertebrata, as Dohrn has lately done. But the physiological side of the question is not touched by it; it is this: Why could only exactly four extremities be developed, and not six, eight, or more out of this skin-fold? Thacker does not go into this question. Dohrn certainly thinks he has found the use of the number four as applying to the limbs; according to him a long narrow fish swims best when it possesses two pairs of fins as far as possible from each other, one pair in front and one behind.

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This idea at first seems striking, but it is opposed alike to the facts, and to the laws of mechanics.

Note 6, *page* 37. With reference to the constancy of such characters as have arisen under external influences, Sachs says, in his *Text-book of Botany*: 'We may infer very decidedly that hereditary characters, or such as might become hereditary, are not produced by external elementary influences, from the fact that seeds from the same fruit produce several varieties, or one variety side by side with the hereditary parent-form;' and further on: 'We come to the conclusion that hereditary varieties first arise independently of direct external influences, but that the possibility of their continued existence depends on such influences.' There can certainly be no doubt that a great number of modifications which are in a high degree hereditary were due to causes which—like sexual reproduction and hybridisation—we are not accustomed to designate as external influences, although I reckon them as such; and it is equally little doubtful that those conditions which are universally recognised as external—such as climate, nutrition, the nature of the soil, &c.—are able to acquire a modifying influence on living and growing animals; thus the modifications called forth by such causes must constantly recur as long as the causes themselves remain constant. In the course of our investigations I shall have occasion to discuss a few examples which may be regarded as having a direct bearing on this. So far as I know, it was Helmholtz who first pointed out that the constancy of an altered condition of life must result in the permanence of any deviation from the parent form of the species—or of the organ—to which such an alteration had given rise.

Note 7, *page* 38. I need here adduce only a few quotations. 'There can be no doubt that changed conditions induce an almost indefinite amount of fluctuating variability by which the whole organisation is rendered in some degree plastic' (Darwin, *Descent of Man*, i. 114). 'Such changes are manifestly due, not to any one pair, but all the individuals having been subjected to the same conditions' (Darwin, *ibid.*, in speaking of horses, page 236); and finally, 'We do not know what produces the numberless slight differences between the individuals of each species, for reversion only carries the problem a few steps backwards; but each peculiarity must have had its own efficient cause. If these causes, whatever they may be, were to act more uniformly and energetically during a lengthened period (and no reason can be assigned why this should not sometimes occur), the result would probably be not mere slight individual differences, but well-marked, constant modifications (*ibid.* p. 153). And in other places in the same book, as well as in his other works, Darwin expresses himself in a way that proves that he no longer rates the influence of the conditions of life (external causes) on the transformation of forms (in species as in organs) so low as he seemed to do in the first edition of his *Origin of Species*.

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CHAPTER II.

Note 8, *page* 40. Hitherto only one single genus of animals is known of which the species are occasionally able to go through their whole cycle of development without their requiring to take nourishment from the time they escape from the egg till their death. The male individuals of some species of *Ixodes* never take any food after they have left the egg, and they perish after fulfilling their sexual function. Hence the amount of food contained in the egg must have been sufficient for the requirements of the creature throughout life.

Note 9, *page* 41. Numerous instances are known of such long-enduring resistance to want of food in the Invertebrata as well as in the Vertebrata. In this respect those snails must be mentioned which were kept for years with their shells glued down, in the collection in the British Museum, and at last, under specially favourable meteorological conditions, were enabled to creep away. At all times those cases have excited much attention which have seemed to prove that Amphibia, such as toads, salamanders, &c., have been preserved from the remotest times, though shut up in a perfectly hermetically closed stone. But the data in these individual cases are always so far from exhaustive that it is impossible to found any explanation on them; it therefore seems to me superfluous to give here any special cases, and I refer the reader to the literature of the subject given by Schmarda (*Geographie der Thiere*, vol. i. p. 101).

But it is highly probable that they all, without exception, might be explained in the same way as a case described by Frauenfeld in the year 1867. A stone of about the size of the palm of the hand had in it two cavities which communicated with each other, and in one of these an Amphibian about two inches long—probably *Triton cristatus*—was living curled up when the stone was split open. The cavity communicated with the outer air by a small hole, which was 1 millimètre (about $\frac{1}{25}$ of an inch) in depth, and about 3 millimètres wide. Frauenfeld assumes that the larva found its way into the inner cavity, there grew, and at last became too big to get out again. It had, moreover, not been able to obtain enough food (it was apparently at least a year or two years old) to grow beyond two inches in length. According to this the *Triton* had not, however, been absolutely without food; but we may regard it as quite certain that it had obtained a very insignificant amount of nourishment, since through so narrow an opening it was impossible that it should have been supplied in sufficient quantity. Experiments have even been made on this matter, for living amphibia have been enclosed in masses of gypsum, and left thus enclosed, and they have

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lived more than a year. However, so far as I know, no satisfactory series of experiments have been carried out to the end.

Note 10, *page* 43. Even the statements in handbooks (see Milne-Edwards, *Leçons d'Anatomie comparée*, viii. 169, 184) or in special treatises, as to the requisite maximum (or optimum) of the amount of food, show great errors, because it is impossible to obtain by experiment any perfectly satisfactory information as to the relations of consumption and ejection. Thus Hermann says: 'Even far more uncertain are the statements as to the absolute amount of the minimum of excretion or the minimum of food required to cover it, in consequence particularly of the uncertainty of the methods of inquiry formerly pursued;' and he therefore forbears mentioning any absolute figure for the minimum of assimilated matter, as ascertained by these methods. Moreover, the subject has never been, to my knowledge, treated from any more general point of view than a purely medical one. Thus, for instance, the fact that a kilogramme weight in a pigeon needs more nutrition than the same weight in a dog, and this, again, more than a kilogramme in a man, is explained by a reference to the greater energy of the vital processes in the smaller organisms. This argument is just, if it is confined to the warm-blooded animals, but it is false with regard to the cold-blooded animals; for as, in these, the variations in the temperature of the body agree perfectly, or very nearly, with those of the surrounding medium, water or air, no more warmth need be produced in the small animals than in the large, nor need a correspondingly larger amount of nourishment be consumed. Beyond this we know absolutely nothing of their relations in cold-blooded animals.

Note 11, *page* 50. At p. 46 a similar example was mentioned, where I pointed out that the assimilation of food in *Limnæa stagnalis* did not depend merely on the circumstance of the food being obtainable in sufficient quantity and of suitable composition, but also on the osmotic action of the skin itself. If the temperature is too low, below 12° C. for instance, assimilation ceases in these snails although they continue to feed; at 20° C. the greatest proportion of food is digested and the most rapid growth attained. But even then, this only takes place when the influence of the volume of water, which can only be exercised by the osmotic action of the skin, is exercised in the most favourable manner. For more details on this point see Chapter V. and the notes.

Note 12, *page* 60. For all who think that the number of cases mentioned in the text are insufficient evidence for the position here advanced, I here briefly give a number of other similar ones. Eels, which usually live on animal food, will also eat bread. Spiders feed almost exclusively on Articulata; a few species, as our European *Atypus Sulzeri*, feed on snails; the tropical species of *Mygale* are said to eat small birds; here in Würzburg, I and Menge fed them with young mice. The Loach,

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Cobitis fossilis, which is specially adapted to animal feeding, frequently eats species of *Lemna*. Many caterpillars, among the Noctuidæ—for instance, species of *Agrotis*—eat each other if they are shut up together in a box, though in freedom they feed only on roots and leaves. The larvæ of the common frog eat plants, the full-grown frogs only insects, worms, or even amphibia. All apes, although their teeth are apparently adapted to a fruit or vegetable diet, are passionately fond of animal food, as birds, eggs, insects, &c.; they will even gnaw bones. Many parrots eat butter, bacon, lard, snails, raw eggs, beetles, the brains of small birds, and marrow. Most Nematoda live as parasites in animals, but a few live in plants—*Tylenchus tritici*, for instance, which lives in the flower of wheat, and *Tylenchus dipsaci*.

Most Holothuriæ shovel sea-sand into their mouths with their tentacles, and leave it to the intestine to select the organic particles of nutriment that are mixed with it. *Thyonidium molle*, on the Peruvian coast, feeds, on the contrary, on sea-weeds. Almost all Hymenoptera are phytophagous, excepting only a few wasps and hornets, and ants which feed on dead flesh. Certain snakes—*Leptognathus* and *Amblycephalus* (see Günther, *Ann. Mag. N. Hist.* 1872, ix. 29)—feed on snails, while all other species eat vertebrata or sometimes minute insects. *Cyclura lophoura*, a species of iguana-like lizard in Jamaica, is herbivorous, although it belongs to a carnivorous group. Most tortoises live on animals; only a few land tortoises eat vegetables. All birds of prey feed on mammals, birds, or reptiles; but the secretary-bird, that stalks about on long stilt-like legs like a heron, rummages about in the mud, like a duck, for aquatic creatures of all kinds. One of the most interesting examples is afforded by the genus Onchidium among the pulmonate mollusca. The lingual tongue of those mollusca which live exclusively on animal food is very sharply distinguished from that of the herbivorous species; a few of these last, as *Limnæa stagnalis*, are, no doubt, carnivorous also (see p. 59 of the text); but in general we may consider ourselves justified in determining those molluscs as herbivorous of which the rachis has the same structure as those of *Helix* or *Limnæa*. All the species of Onchidium which I have hitherto been able to examine, about four-and-twenty, have exquisite herbivorous teeth, and, nevertheless, do not use them for eating off plants, but exclusively for shovelling in sea-sand or mud. Hence we see that even the organs of mastication, which yet must be quite specially adapted to the nutriment obtainable at the time and to the mode of obtaining it, may under some circumstances be used in very various ways; and we must therefore conclude that in comparing living creatures with fossil ones these organs can afford no absolutely reliable means for determining the food and mode of life of these primeval creatures. These exceptions, moreover, afford us a further example of the proposition stated in the text, that even organs which appear to us to be adapted to a special office are never-

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theless able, and by their internal nature must be able, to accommodate themselves to others.

Note 13, *page* 64. It seems to me desirable to add a few more instances of voluntary change of food by monophagous animals to those given in the text. The palm-crab, *Birgus latro*, in a free state feeds on fruits, namely cocoa-nuts, but in confinement eats its fellows (as I know by experience). Canary birds, and fowls, often and readily eat lard. The American prairie dogs Hans and Gretel, which I have already mentioned in the text, quickly accustomed themselves to a diet of fish, which was wholly unknown to them, with mollusca and meat. I owe to my friend Professor Hagen (of Cambridge, Mass. U.S.) the following interesting notes. At Cape Cod, the cows are regularly fed on herrings' heads; in Norway a mash is prepared for the cows by mixing and stirring horse-dung with the heads of dorse boiled down; this serves them for fodder only in the winter; in the summer they eat grass, as they do everywhere else. The reindeer, according to Brehm, sometimes eat lemmings.

Note 14, *page* 68. The change of structure which takes place in the stomach of the pigeon and the gull in consequence of the change of function is as follows. The stomach of a bird subsisting on flesh has a comparatively feebly developed muscular layer and a soft mucous membrane, which penetrates the coats of the stomach, forming long tubules; these tubules are the glands which secrete the gastric juice. In the grain-eating birds the muscles of the stomach are particularly strong; instead of the soft mucous membrane a thick brown membrane covers the inner surface of the larger part of the stomach, while the small anterior portion exhibits the same soft skin and glandular layer as are everywhere distributed in the stomach of birds of prey. This brown skin in the gizzard of the pigeon (see fig. 13) is very strong; it has long fine filaments which penetrate the cavities of the tubules which extend perpendicularly into the muscular layer of the stomach. Now, if the stomach of the pigeon is acted on for a sufficiently long period by feeding on flesh, this brown skin (called a cuticula) withdraws entirely from the tubules and is ejected; the tubules now no longer secrete any solid matter, but only a fluid, and so become true glands. It would be interesting to ascertain whether the secretion now produced by these in the gizzard is to be compared, chemically and with respect to its digestive qualities, to the gastric juice in the stomach of birds of prey. In gulls, on the other hand, which have become accustomed to a grain diet, the hitherto fluid secretion from the glands opening into the stomach becomes rigid, and a more or less firm thick skin is formed in the interior of the stomach.

From the text it might perhaps be inferred that the stomachs of graminivorous and of carnivorous birds were two distinct forms of stomach corresponding uniformly and exactly to these modes of feed-

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ing, so that the former occurred only in birds that feed on grain, and the latter in those that feed on animal food. This, however, would be an error, since there is a considerable number of flesh-eating birds of which the stomach (the muscular stomach, as it is called) is constructed exactly like that of a pigeon or a hen. *Podiceps minor* (the little Grebe) lives on fishes, worms, and soft-bodied aquatic creatures. *Corvus Cornix* (the hooded crow) and *C. Corax* eat insects, birds, and small quadrupeds. The lapwing lives on soft aquatic animals, and the kingfisher on fish. In all these the muscular stomach has quite as thick a muscular layer as in the pigeon, and the internal coat is a hard, brown pseudo-cuticle, such as is always present in the graminivorous birds. Even among true birds of prey some have the pseudo-cuticle, at any rate for a time—as the recently fledged kestrel—though not, it is true very strongly developed. In these birds a meat diet does not seem to effect so rapid a change in the stomach—from a graminivorous to a carnivorous type—as in the gull and the pigeon, nor, indeed, to affect them in any way.

Note 15, *page* 69. In the text I have not mentioned a number of effects of food which in part are not suited for discussion in a popular lecture, but in part too have no bearing on the question we must steadily keep before us, *i.e.* how far the maintenance of the species or the origin of new forms may be induced by them. Thus, for instance, Voit's experiments on the assimilation of fresh-water mussels seem to have established beyond a doubt that the greater part of the ashy constituents of their bodies, which they deposit almost exclusively in their shells, are derived from the water which, according to him, is taken up by the kidneys. But then the question as to how the water penetrates the body of the mussel is still under controversy. Some authors entirely set aside the old view that the kidneys, wholly or in part, have the function of absorbing water: according to them it takes place through pores in the skin; but this, notwithstanding all that has been said on the subject, is not absolutely beyond dispute. In fact, so long as the morphological bases of physiological speculations are as little assured as in this case, any discussion must be regarded as premature.

The second point, to be here only lightly touched on, regards the influence of food on the sexual functions and in the external distinctions of sex which partly depend on it. It is known that certain foods or stimulants at the approach of sexual maturity have a stimulating effect on the secretion of the semen. Too small a supply of food is as injurious to the germinal glands as too large a one; for this predominantly important side of animal life, also, there is an optimum of nutrition, and any excess towards the maximum, or deficiency towards the minimum, must exert a proportionally injurious influence. Unfortunately we know of hardly any serviceable experiments on this subject,

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for those made on domestic animals can scarcely be regarded as such, since their results cannot be considered applicable to other animals living in a state of nature. Sanson has lately made some very interesting experiments on domestic animals, which seem to prove that sexual maturity can be very much hastened by a careful and special hygiene, by an increased amount of nourishment and by the addition of certain substances to the diet. (Sanson, *Comptes Rendus*, 1874, lxxix. 1768; and *Journal de l'Anatomie et de Physiologie*, 1872, p. 113.) The animals thus brought up are said to assume a quite special development—to become races; the signs of their earlier development and precocious maturity are the cutting of the permanent teeth and the growing together of the epiphyses (the osseous portions of the hollow bones) at an age when, in animals fed in the usual manner, these tokens of approaching maturity are not yet visible. As we shall presently see, precisely similar effects follow from raising the temperature. In conclusion I will only mention that Von Willich states that in frogs a deficiency of food causes darker colouring of the skin.

CHAPTER III.

Note 16, *page* 70. A comparison of the eye of the animal and the chlorophyll bodies of plants as standards of equal value for estimating the intensity of light was, in fact, attempted by Prillieux. Sachs has controverted this attempt in his usual brilliant and thorough way, and has set it aside, let us hope, once for all. 'All comparisons as to the intensity of differently composed light, made by means of the eye, have, from the nature of the eye, no independent value.' Hence the intensity of the different colours of the spectrum as thus estimated cannot be made use of to measure the gas disengaged by plants by means of the chlorophyll bodies, as Prillieux has done.

Note 17, *page* 72. I here give a complete list of those species of animals in which chlorophyll or similar bodies—as xanthophyll, &c.—are said to occur.

Protozoa:

Euglena viridis.
Stentor viridis.

Almost all Radiolaria. But among the marine Radiolaria most of the Acantho-metridæ are excepted (Haeckel, *Monograph of the Radiolaria*); and among the fresh-water Radiolaria, *Actinophrys*, *Actinosphærium*, &c.

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Not to be confounded with these chlorophyll-bodies of the Protozoa are certain peculiar green or olive-green discs of colouring matter which occur in many Monadinæ, as for example in *Chromulina, Chilomonas, Paramecium, Uvella virescens, Mallomonas Ploeslii*, &c.

Spongilla viridis (Sorby, *Quart. Journ. Mic. Sci.* 1875, vol. xv. p. 47.)

Cœlenterata: *Hydra viridis.*

Platyelmia: *Vortex viridis.*

An undescribed marine Planarian, according to Geddes. It is stated that this creature decomposes carbonic acid; no exact report, however, has as yet been given, so that it is not possible to decide whether this statement rests on experiment or is only inferred from observations, which alone prove nothing.

Gephyrea: *Bonellia viridis* (Rolando). Schenk says that the green colouring matter of this worm is true chlorophyll. Sorby, however, (*Quart. Journ. Mic. Sci.* 1875, lviii. p. 166), after a very careful investigation, proves that this matter is quite distinct from chlorophyll.

Leydig has lately propounded the hypothesis that chlorophyll may occur even in insects. He founds it on the observation that the vivid green of various beetles, orthoptera, &c., changes towards autumn in the same way as the leaves of trees do. I regret that I cannot agree with him on this point; no such conclusion can be derived, in my opinion, from the observed phenomena. The view that insects can themselves elaborate chlorophyll cannot be supported by any argument, and it is equally improbable that chlorophyll, as such, can be stored up from the food in the circulating system of an insect, and then deposited in the skin without being wholly altered; but even if after this process it could preserve its green colour and other original properties it must certainly have lost the characteristic property of chlorophyll, namely, that of decomposing carbonic acid under the influence of light.

Note 18, *page* 76. Foreign bodies occur by no means rarely as integral constituents of the tissue of animal organisms. Irrespective even of those cases in which parasites become normal (*i.e.* constantly present), constituents of certain portions of the body in every individual of a species—as for instance the Nematoda living in the foot of certain naked mollusca—there are numerous other examples. Among the Cœlenterata there are, besides *Sphenopus*, various other genera which take up grains of sand directly into their skin—for instance, all the Zoanthinæ (*Zoanthus, Palythoa*, &c.)—whereby it acquires the firmness it would otherwise lack. The sponges often have the habit of including foreign siliceous particles, the calcareous shells of *Polythalamia*, fragments of corals and of the shells of molluscs, or merely sand, in their horny fibres; such foreign bodies occur in by far the larger number of keratose sponges. That the siliceous spiculæ are in these cases very often merely foreign bodies is proved by the circumstance that they are found without excep-

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tion with broken points, and this could not be the case if they were formed in the horny fibres by the creature itself. Since the horny tissue, even in living sponges, is much too tough passively to allow of the intrusion of foreign bodies during the life of the sponge, their being imbedded in the fibre can only result from the sponge drawing them to itself by a voluntary act and including them between the layers at the growing apex of the horny fibres. One of the most remarkable instances of the utilisation of foreign bodies as an integral constituent of an animal structure is offered by the species of *Xenophora* among the mollusca; they voluntarily incorporate into their shells, in regular order, other shells and fragments of stone or of coral. Their intimate adhesion shows that this combination must be effected before the shell has hardened, and each particular species of Xenophora seems also to have more or less choice among the materials at its disposal. Bergh has recently shown that *Staurodoris Januarii*, a naked marine mollusca, eats the spiculæ of sponges and deposits them in its skin.

We may here allude to the use made by the larvæ of the *Phryganeidæ* of leaves, snail-shells, roots, &c., in building their cases (caddis-worms).

The above-mentioned regular association of two kinds of animals, one of which lives in or on the other as a constant parasite, offers many remarkable phenomena. It is known, for instance, that the hermit crab (*Pagurus*) is sometimes infested by dark-brown Crustacea of the group of the *Rhizocephala*; when these are present the female germ-glands never develope in the host, and eggs and parasites are never found together in the same individual. In certain localities the parasites are so common that out of hundreds of hermit crabs scarcely a single individual will be found without one, although their numbers are no less than in other spots in the vicinity where there are no parasites, or hardly any. This proves that the growth of the *Pagurus* is not in the least hindered by the foreign parasite, while the development of sexual maturity is wholly arrested; and we see, moreover, that the conditions for the reception of the parasite or for its avoidance may be quite different in two contiguous spots.

I myself have made similar observations with regard to *Limnæa stagnalis*. The larvæ of Trematoda which infest these water-snails, in the first place at any rate, and almost exclusively, as it would seem, destroy the germ-glands, but they do not check the creature's growth. In however great a number the parasites may be present, the mollusc grows all the same, but propagation is completely prevented. How far the sterility thus induced in certain individuals may possibly give rise to other changes in their external or internal conditions is wholly unknown, and has not been investigated. The larva of a fly, *Cuterebra emasculator*, destroys the testes of various American species of squirrel without affecting the other vital functions; and the number of such

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animals, healthy in all other respects, annually shot by hunters seems to be very considerable. (Dr. Hagen.)

Note 19, *page* 78. There are but few totally blind vertebrata—absolutely deprived, that is to say, of eyes. All the species of mole have rudimentary eyes, as have the Proteus and the blind-fish, as they are called, of the American caves; *Amblyopsis spelæus*, *Typhlichthys subterraneus*, *Stygicola dentatus* and *subterraneus* (from caves in Cuba), *Gronias nigrilabris*, *Stygogenes cyclopum*—or of the caves of Asia, *Ailia*, *Shilbichthys*, *Bagroides*, &c. Actually eyeless fish have hitherto been found only at great ocean depths, and we owe our knowledge of them to the 'Challenger' expedition. They are *Scopelidæ* or *Lophioidæ*. What makes them especially interesting is the occurrence of the peculiar organs on the head, first observed by Von Willemoes-Suhm, and subsequently accurately described by Günther, who regards them as organs of phosphorescence (see note 22). Truly blind invertebrate animals are far more numerous. Most ento-parasites are perfectly eyeless. The number of species of blind cave-insects, which is being added to every day, already amounts to hundreds. The reader who is specially interested in these creatures will find a very complete review of the literature of the subject in an admirable paper by Simon and Bedell in the *Revue Zoologique*. Associated with the blind cave insects we find blind spiders, Crustacea, and Myriapoda; the blind crab of the Kentucky caves has, according to Hagen (*Monograph of the North American Astacidæ*), certainly only rudimentary eyes; while other Crustacea, as *Cœcidotea*, *Stygia*, *Titanethes albus*, and others, seem to be totally blind. In the work of Putnam and Packard on the Mammoth Cave of Kentucky there is a list of these forms with excellent illustrations. Various Crustaceans which are called blind are known from the caverns and subterranean waters of Europe; to these belong *Niphargus puteanus*, *Titanethes albus*, *Crangonyx*, *Asellus Sieboldii*. Univalves seem always to have eyes, with the exception of a few which live as parasites, but a *Hydrobia* found living in Munich by Rougemont, and which inhabits deep springs, seems to have no eyes. Wiedersheim found rudimentary eyes in the Hydrobia of the Falkenstein cavern.

The 'Challenger' expedition also has furnished us with rich materials on this subject. Willemoes-Suhm, whose premature death we must deeply deplore, made us acquainted with a large number of peculiar blind Crustaceans, some of which live at a depth of more than 2,000 fathoms; for instance, *Petalophthalmus* of various species, all the *Munopsida*, several *Mysideæ*, several blind larvæ belonging to the *Zoea* and *Megalopsis* forms, *Astacus zaleucus*, *Aspendes cæca*, *Dcidamia*, &c. Notices of these occur in the narratives of the voyage communicated to *Nature*; *Ann. and Mag. Nat. Hist.*; *Proc. R. S.*; *Linn. Soc. Trans.* And a tolerably complete guide to the literature of the subject is to be found in Siebold's supplement to Willemoes-Suhm's *Challenger-Briefen*

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(*Zeitschrift für wiss. Zoologie*, 1877, v. 27). The recent treatise by Pagenstecher, *Ueber die Thiere der Tiefen*, also contains a list of blind as well as other deep-sea animals, though in a somewhat different arrangement from that which I have given here.

Note 20, *page* 82. The following animals, furnished with well-developed eyes, live in caves: *Machærites*, 7 species (Coleoptera); *Anthomyia, Phora* (Diptera); *Hadenœcus*, 2 species (Orthoptera); *Spirostrepton*, several species in caves (Myriapoda); *Nesticus*, 2 species; *Linyphia*, 3 species (Spiders in the Kentucky caves). Animals having only rudimentary eyes must be partly included here. A *Melania* having eyes I myself found in a cave in the Pelew Isles, and in the same spot was a grasshopper that could see. Also among fishes, *Chologaster Agassizii* (in Kentucky), *Umbra Crameri* (in subterranean lakes in Austria, according to Schmarda, *Geog. der Thiere*, i. 13). In the caves of Utah (according to Packard, *Bulletin N. S. Geol. and Geog. Survey*, iii. 1877), a Phalangium—*Nemastoma troglodytes*—with eyes; a Univalve, *Hyalina subrupicula*; and a Podurida, *Tomocerus plumbeus*, equally with eyes, are associated with a blind Myriapod, *Polydesmus caricola*. Fries states that the blind *Gammarus puteanus* of the Falkenstein caves sometimes quits the regions of absolute darkness.

Note 21, *page* 84. Many creatures furnished with well-constructed eyes live associated with the actually blind species which have been partly enumerated above. An attempt to account for this apparent contradiction is mentioned in the text. Of the very considerable number of such denizens of the darkness which nevertheless can see, I will particularly mention the following: *Bathytroctes*, a new genus named by Günther, 675 to 1,090 fathoms; *Bathylagus*, 1,950–2,040 fathoms; *Platytroctes*, 1,500 fathoms; *Chlorophthalmus gracilis*, 1,100–1,450 fathoms—all forms of Fishes discovered during the 'Challenger' expedition. Besides these, among Fishes, *Macrurus* and *Halosaurus*, 1,375–1,600 (Willemoes-Suhm, *Challenger-Briefe*); among mollusca, *Chiton* and *Patella*, 1,075 fathoms (Willemoes), *Pleurotoma*, n. species, 2,090 fathoms, and *Fusus* sp., 1,207 fathoms (Thomson, *Depths of the Sea*, p. 465); Crustacea, a *Palinurus* in 700 fathoms; a *Neyhrops* and an *Amphion*, between 1,875 and 3,125 fathoms. Various crabs, *Galathea, Calappa*; Isopoda, *Serolis*; Macroura, *Penæidæ, Caridida*. *Bathynomus giganteus* (M. Edw.), a gigantic Isopod 23 centimètres long, having large eyes, each with 4,000 facets, and others. It is impossible here to give a complete list, nor is it within the purpose of this work. Other deep-sea forms have rudimentary eyes, as, for instance, *Aphyonus gelatinosus*, 1,500 fathoms; *Typhlonus nasus*, 2,150 fathoms, from N.E. Australia, &c.

Note 22, *page* 85. Phosphorescent creatures are extremely common on the surface of the sea, as is well known. They belong to the most various classes but are for the most part invertebrate animals, Infusoria,

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Medusæ, Polyps, Worms, Tunicata, &c. Phosphorescent fishes have been brought to our knowledge by the 'Challenger' expedition. Willemoes was able to observe directly the phosphorescence in *Sternoptyx*; and according to Günther (see below) it is highly probable that the peculiar organs occurring in blind fishes are phosphorescent. The fishermen of Nice assert that the moon-fish, *Orthagoriscus mola*, is luminous. But few phosphorescent animals live on land; only a few Myriapoda and Annelida, besides the well-known Lampyris, Elateridæ, &c. The literature of the subject is wonderfully extensive; Ehrenberg, who gave more attention to it than almost anyone else, in the last year of his life gave us a work with the following title: *Die das Funkeln und Aufblitzen des Mittelmeeres bewirkenden unsichtbaren Lebensformen* (Berlin, 1873).

Note 23, *page* 86. The anatomy of the fishes in which Günther found these phosphorescent organs is not yet described, and I owe the notice I am enabled to give to a verbal communication from my esteemed friend in London.

Note 24, *page* 89. See on this subject the brief remarks in Sir Wyville Thomson's *The Depths of the Sea* (ed. 2, p. 465). Many observations on the brilliant colouring of Holothuridæ and Crustacea occur in Willemoes' reports. This proves that the lack of light cannot directly hinder the development of pigment. But it is quite possible that it may have an indirect influence through modifications in the processes, at present unknown, which lead to the formation of the pigment.

Note 25, *page* 89. Higginbottom, 'Influence of Physical Agents in the Development of the Tadpole of the Triton and the Frog,' *Phil. Trans.* 1850, p. 431. He reared larvæ in dark cellars and in complete darkness without discovering any difference in their development beyond its retardation by the diminished warmth.

Note 26, *page* 91. Within the last few years I have repeated a series of experiments with a view to investigating the effects of different light on the formation of pigment in animals; the creature selected for the purpose was the Axolotl. The more general results attained by these experiments are given in the text. The origin of the pigment does not depend directly on light, as Bert states, nor do albinos or white Axolotl occur in the dark. It remains a mystery to me how Bert could have ascribed the occurrence of white Axolotl to the influence of a deficiency of light, and I am equally ignorant as to the causes which led to the production of albinos among the Axolotl kept by Kölliker at Würzburg.

I found, precisely on the contrary, that when the light was excluded, or in a dark red light, the young animals were always dark-coloured; in a yellow light the pigment was abundant though less dark; in a white diffused light, but to the exclusion of the direct rays of the sun, they were of a much lighter hue, but still not white.

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Specimens which I kept for a year and a half in white vessels, and as close as possible to a window with white blinds, assumed a very light yellow-green colour in which a very few scattered specks of black pigment could be detected; but the small silvery spots which sometimes appear on these creatures when about six months old attained so large a size, particularly on the tail, that the animal might be described as yellow-green with silver spots; in some cases the silver spots predominated. In young specimens of this year's brood, which were also from the first reared in a diffused white light, the green colour is already beginning to show, and the silver spots also on the larger specimens on the face of the external branchiæ. (This is in August; the young Axolotl are about 50 days old, and the larger-sized ones about 7 cent. long.) These results of my experiments agree tolerably well with those of Pouchet and Lister if we assume that the colouring of the Axolotl is produced entirely by the action of chromatophores. The black pigment and the silvery hue, at any rate, appear to reside in such cells, but the pale yellow-green ground hue of the specimens kept in a white light appears to result from a pigment distributed and diffused throughout all the organs. Hence any pronounced adaptation of colouring to the surrounding objects such as occurs among fishes and crustaceans is certainly not in question, and nevertheless the whiter light induces paler colouring.

The pigment of butterflies of which the pupæ lie buried in the earth is developed in total or almost total darkness before they escape; the chitinous skin of many pupæ (of moths, &c.) is so dark as to be almost perfectly impenetrable to light; nevertheless pigment of very various characters developes in them. We may, indeed, presume that in most viviparous animals the development of the embryo takes place in total darkness; nevertheless they are all born with bright colours. Here too must be mentioned the observation made by Kerbert that in the embryo of the chick certain pigment cells which appear in the cutis about the fifteenth day have wholly disappeared by the twenty-third. It may be supposed that not much light, or none indeed, can penetrate to the embryo through the egg-shell and membranes; nevertheless, pigment cells are formed and disappear again during the course of the embryo stage. No explanation of this remarkable circumstance has as yet been given. It is not uncommonly supposed that the presence of a dark pigment in the skin of human beings is due to the greater intensity of light, as proved by the predominance of dark races of men towards the equator and by the darkening of the skin in summer. As, however, no experiments are before us by which the chemical or heat rays have been excluded from acting on the skin at the same time as the light rays, while the action of the air and that of difference of nourishment have remained disregarded, we cannot consider the conclusion as proved, or even admissible, which asserts that

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the development of the skin-pigment is influenced by light, even with regard to man.

Note 27, *page* 92. Heincke describes the colours of *Gobius Ruthensparri* as follows: 'In the first instance a black velvety spot is conspicuous lying at the base of the caudal fin and surrounded by a beautiful golden-yellow margin. A similar black spot, but without any yellow rim, is found in the male, on each side, at the base of the pectoral fin; this is absent in the female. The ground-colour of the back of the male is, in the breeding season, of a dark brownish black, cutting in on the green; on the head it is lighter with a reddish tinge; there are five light-coloured saddle-shaped spots with a metallic sheen, and the under-surface of the head is of a vivid copper-colour with a golden gleam. On each side, between the light and dark colour of the body, and rather below the lateral line, there is a row of vivid spots as bright as jewels, glittering now blue, now green, and there is a similar spot on each gill-covering, which is otherwise red. The two dorsal, the caudal and the anal fins are cherry colour and yellow, or show green stripes and bands on a dark ground. The pupil of the eye shines a deep blue.' To this somewhat abridged description he adds: 'I have given these elaborate details that the reader may form some idea of the beauty of the *Gobius* at certain moments, for all this gorgeous colouring may vanish within a short time and not return in its pristine splendour for a long time.' He then fully describes the chromatophores and their function.

Note 28, *page* 97. Dewar, 'The Physiological Action of Light,' *Nature*, 1877, p. 433.

Note 29, *page* 99. Darwin himself frequently uses the word 'colour' where 'distribution of colours' or 'mode of colouring' would be better. Still it is always clear from the context that he attributes to origin through Sexual Selection only such variations in colour as occur for instance in the male and female of the same species, and to Natural Selection such as have proved a protection, and therefore advantageous to animals. To assume colouring, *i.e.* the determined mode and arrangement of colour, is to assume the pre-existence of colour; the question as to how this originated has never, to my knowledge, been inquired into in these later times, and perhaps it is for this very reason that it has frequently been confounded with the origin of the mode of its distribution. (Compare Darwin, *Descent of Man*, chap. on Sexual Selection.) Other naturalists, at any rate, have certainly made this confusion. Thus, for instance, the variation of green to brown which is exhibited by many Sphinx-caterpillars has been attributed to natural selection (see Weismann, *Studien zur Descendenz-Theorie. Die Entstehung der Zeichnung bei den Schmetterlingsraupen*, p. 80). Selection, however, could not possibly effect any alteration in the pigment, but could only operate after such a change had actually occurred.

Note 30, *page* 100. There are many works, not here referred to, on

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the effects of light on the animal organism. Some are of too special a nature and too exclusively addressed to medical physiology—as, for instance, the observation that frogs disengage more carbonic acid in a green light than in a red one; those on the dependence of the colour of the skin on certain constitutional diseases, &c., while some are not sufficiently detailed to allow of their being used here. To these belongs, for instance, Strethill Wright's observation that polyps of the higher Acalephæ are said to multiply abundantly in the dark by buds, while in the light, and with insufficient supplies of food, they bring forth Medusæ. To these also belongs all that has been said of the dependence of lighter or darker tones of colour on the various intensity of light. Thury's observation that, under a green light, tadpoles retain their gill-respiration, while their legs are not formed, and that finally they die, comes under the same category. Likewise the phenomena of melanism and hyperchronism (see Ridgway, 'On the Relation between Colour and Geographical Distribution in Birds;' *Silliman's Amer. Journ.*, ser. 3, vol. iv., 1872, p. 454), which are attributed sometimes to the influence of heat or of light, and sometimes to the general climate. The statement, too, that white rabbits are most easily and certainly reared in a white reflected light, is worthy of attention. I owe this remark to Dr. Braun of Würzburg, who met with it recently in an agricultural journal. In this case, as in all cases of experiment, it is requisite to distinguish between the different causes, and to investigate separately the effects of each. Hitherto we, the zoologists, have made very light of these physiological labours. Hartmann, and a certain Herr Hesse, declare that a combination of absence of sunlight, cold, and damp, is the cause of the occurrence of albinos (!) among snails; if it is not the one it may be the other.

CHAPTER IV.

Note 31, *page* 104. The method of meteorological diagrams could at most be applicable to cases uninfluenced by annual and diurnal variations of temperature; as those of creatures living in the depths of the sea or of fresh-water lakes, in deep springs, or in the intestines of warm-blooded animals. And even in these cases such curves would be of no practical application, since we cannot transfer them from the animals for which they hold good at the present time, so as to draw any conclusion with regard to unknown, *i.e.* fossil forms; nor can we form any opinion as to how the creatures living under such equable temperatures would behave if they were suddenly or gradually exposed to the effects of a different degree of heat. In point of fact, the application of climatic curves—even in its more limited form—has only hin-

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dered the progress of our knowledge of the real effects of temperature on the life of animals.

Note 32, *page* 105. 'In the shallow seas of temperate latitudes, only such animals can exist and preserve their reproductive powers as are qualified to endure every variation of temperature which may occur in the course of the seasons—Eurythermal animals, as they may be designated in one word. The number of eurythermal marine animals is very much smaller than the amount of species which can only live in such provinces (marine) as exhibit an equable or slightly variable temperature—Stenothermal animals, as they have been called.'

Note 33, *page* 109. I must, however, warn the reader against the assumption that every such dwarfed race was produced by the influences here described. In many places, for instance, where formerly really gigantic pond-mussels were found, now only quite small ones occur; and it is well known that the European oysters are gradually becoming smaller. This results from the circumstance that both these mollusca are capable of reproduction while they are still quite small, and now never grow to their full size, because they are destroyed before they have accomplished their full growth. The dwarf races of certain Libellulæ in the south of Europe appear again to depend on other causes. The multiplicity of circumstances by whose co-operation dwarf races are produced appears to be very considerable; we shall have occasion to examine them somewhat more closely in another chapter. Unfortunately no satisfactory experiments have ever been made.

Note 34, *page* 110. Winter-sleepers—*i.e.* animals which during the winter fall into a dormant state, and remain in it for weeks, or even months, without dying—are to be found in almost every group. I may refer the reader to the enumeration given by Schmarda (*Thiergeographie*, i. 9–11). It might be well to distinguish two groups of such animals, according to whether they are warm-blooded or cold-blooded. These last—as we infer from some observations merely, it is true, and not from experiment—appear to possess the faculty of living a latent life at a very low temperature, *i.e.* to sleep; and if we suppose that no alteration takes place in the processes of assimilation, but only a retardation, every cold-blooded animal might fall into winter-sleep. With warm-blooded animals it is otherwise. These, as is well known, are easily frozen; according to Horvath's experiments—to be more exactly described presently—it is extremely probable that no warm-blooded animals can become winter-sleepers but those which are able to become actually cold-blooded at a sufficiently low temperature. Even young animals of other species which have at birth a remarkably low temperature, almost as low as that of cold-blooded animals, are incapable of enduring low temperatures for any length of time; they fall asleep, it is true, but at the same time they die. Of course, even the winter-sleepers among mammals cannot bear to be actually frozen.

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Note 35, *page* 111. The high body-temperature of the true warm-blooded creatures, birds and mammals, oscillates within very narrow limits. In man it rises to 36–38° C.; in dogs to about 39°; in the sheep to 40° or rather more; in birds it is higher, rarely under 40° and usually as high as 42° to 43° C. (For very ample data see M. Ed. *Anatomie et Physiologie Comp.*, viii. pp. 16–18.) In cold-blooded animals even it is always a little higher than that of the surrounding medium, but it rises and falls with this, while the true warm-blooded animals maintain the same, or nearly the same, temperature in spite of the variations in the air or water. How far this may also prove to be the case with such cold-blooded animals as have a temperature considerably higher than that of the surrounding medium has not yet been investigated; we know, for instance, from Davy, that in Bonitos the temperature is 10° C. above that of the water; in *Pelamys sarda*, 5°; according to Czermak, the Proteus of the Adelsberger grotto has an internal heat of sometimes 5·6° C. above that of the water. It may also be mentioned that some species of Python, when depositing eggs, have a body-warmth of 6° C., and that sometimes a very considerable degree of heat prevails in a beehive.

Note 36, *page* 112. The facts given by Horvath are of the greatest interest. The following is perhaps of the highest physiological importance. It is usually supposed that the awakening of winter-sleepers is occasioned by a rising temperature; but in Horvath's investigations this was never the case; during two hours and forty-five minutes, which, in the one experiment communicated, were needed for complete awakening, the temperature of the room remained exactly the same—10° C.—as during the three previous days when the animal was still asleep. This proves that the waking up of the weasel must be caused by some internal cause which we do not as yet know. But his other observation is far more remarkable; namely, that during the awakening, the body temperature of the weasel rises rapidly, and more rapidly during the second half of the process than at the beginning; for instance, in the experiment which is given in detail it rose in the first hour and fifty-five minutes only about 6·6° C., and in the following fifty minutes about 17°. This remarkably rapid increase of body-heat took place, moreover, without any vigorous movements, which might otherwise have been supposed to cause it—even the rapidity of breathing showed no increase corresponding to the rise of temperature.

I must not here pass over in silence the view lately expressed to me by Dr. August Forel, of Munich (well known by his admirable researches on Ants); a view founded on certain observations, hitherto unpublished, that winter-sleep does not depend at all on the diminished temperature in winter, but rather on influences determined by food. A dormouse that he kept went to sleep even at a high temperature of the air, in August and September, and slept as soundly as in a true winter-sleep,

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while its body temperature, according to the figures he was so good as to communicate to me, was never more than a few degrees higher than the air.

Note 37, *page* 112. It is a fact that frogs often deposit their spawn in water hardly above the freezing-point, and a vast number of invertebrate creatures live in equally cold water. These same individuals, however, do not perish when even their body temperature is raised in the summer to more than 30° or even 40°. How far they suffer from it is, however, not established.

Note 38, *page* 114. An enumeration of the observed or reported cases of the resuscitation of wholly frozen animals is to be found in Schmarda's *Thiergeographie*, i. pp. 8 and 98. Insects, fishes, toads, Actinia, Crustacea, Mollusca, and Nematoda figure in this list. It is well known that fish can be conveyed in ice, or even quite frozen up, and revive on being thawed again; but in all these cases the thawing must be very slow and gradual; if it is too rapid the creature dies. Plants exhibit the same characters.

Note 39, *page* 116. It is difficult—in some cases quite impossible—to decide whether the data given are to be depended upon or not; isolated and incidentally made observations are often made to serve as evidence for general statements. Thus it has been said that the Arctic fox is white in winter, and in summer of various colours; but Payne says this is inaccurate, and that *Canis lagopus* may be found white, blue, or grey at all seasons of the year.

Note 40, *page* 117. Weissmann succeeded in transforming all the individuals of a summer brood of *Pieris Napi* to the winter-form by maintaining a low temperature. With reference to Weissmann's estimate of the facts communicated by him as to the rearing of *Vanessa levana-prorsa*, I must observe that I cannot agree with him; interesting as his researches are, they do not seem to me either to have been carried out systematically enough to allow of the deduction of any definite conclusion, nor to prove that the speculations propounded by him are thoroughly well founded.

Note 41, *page* 119. 'Assimilation in plants is only possible between a specific minimum and maximum of temperature; between these two extremes lies an optimum for the development of the species.' So says Pfeffer, and this shows that the same law obtains for plants as for animals. Unfortunately we cannot assert that we have ascertained the curves of temperature for animals, as botanists have already done for many plants. This, it is true, results in great measure from the difficulties offered in experimenting on animals; the phenomena of life are far more complicated in them than in plants, they grow much more slowly and at the same time are far less easy to measure and to confine. However, there are a number of rapidly-growing cold-blooded aquatic animals (water-snails, Naidiæ, Branchipus, Apus, &c.) which are not

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particularly difficult to rear and which can even easily be measured; systematically conducted experiments on them would undoubtedly yield very pleasing and valuable results. Brauer's researches on the Phyllopoda afford a striking proof of this. He found that individuals of a species of *Chirocephalus* lived for weeks in a temperature of 19° C., but never attained sexual maturity; but they acquired sexual functions within two days when exposed to a temperature below 11° C. The eggs of a species of Branchipus could not be induced to develope until after he had strewn them on slowly melting ice broken into small fragments. It is much to be regretted that Brauer has given no exact curves of temperature for the different species he reared; but even as it is, it would seem that we may infer from his remarks that the optima of temperature are often very different for quite nearly related forms.

Note 42, *page* 120. With reference to these animals I must refer the reader to Schmarda's list (*Thiergeographie*). The highest degree of temperature hitherto observed as endurable by any fully grown animal without inconvenience of any kind is 75° C.; in *Sparus Desfontainesii* in the hot springs of Tozer and Cafra in Tunis. Plateau's observations (*Recherches physico-chimiques sur les Articulés aquatiques*, 2me partie, Bruxelles, 1872) only appear to contradict this; for he only experimented on such animals as live in cold water or thermal springs of moderate heat. There is even a certain contradiction between the results of his experiments and the facts he himself records as to the existence of animals in these thermal springs. These springs have, according to Plateau's list, a temperature corresponding exactly to the maximum which can be generally endured by such animals; thus, if we regard his experiments as conclusive, they would live and propagate in a temperature which, being indicated by the extreme limit of the curve constructed to show their power of living, could not therefore be regarded as actually favourable to them. However, the experiments themselves were not conducted on a conclusive plan, for the gradual cooling of the water was not prevented, nor were the investigations carried on for a sufficiently prolonged period. But we must not be led to confound with these certain well-known cases of great resistance to extreme heat exhibited by the eggs of the lower animals, Insects, Rotatoria, Nematoda, &c., or by the capsuled Infusoria, or by certain larvæ. It would seem as though these were thrown into a state of latent vitality—exactly as under conditions of extreme cold —during which their vital functions remained inactive; while in the animals living in hot springs exactly the same processes of assimilation must take place as in those living in colder water. An experimental investigation on an extensive scale of the power of resistance to high temperature in the eggs or germs of the lower animals would certainly amply repay the trouble. Brauer states that the eggs of *Apus cancri-*

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formis and *Branchipus stagnalis* and *torvicornis* may be exposed to the utmost heat of the sun without perishing.

Note 43, *page* 121. Summer-sleepers are found among the most dissimilar groups of animals. The Tenrec of Madagascar (*Centetes*) is well known. Darwin found insects, spiders, snails, toads, and lizards, in a summer-sleep, in Brazil. Most of the land mollusca of the Mediterranean province pass the summer in a dormant condition, and the same is true in the tropics. (Comp. Schmarda, *Thiergeog.* i. 12.) As I have said in the text, in most cases, perhaps in all, the true cause is the dryness of the air which is usually associated with a high temperature. No experiments have been made that can prove that during the summer-sleep the vital processes are not merely reduced to a minimum of energy, but also altered as to their nature—as they are in winter-sleep.

Note 44, *page* 122. It is known that in man for instance, sexual maturity is attained at a much earlier age between the tropics than in northern climates; girls of twelve are in Cuba regarded as fully grown and marriageable. This phenomenon is far more striking in swine. I myself have seen pigs in Manila of which the males at three weeks old were ready and fit to be put with fully grown females. But the great variety of circumstances which co-operate to produce such early maturity leave it doubtful whether it is solely due, as is assumed, to the high temperature of tropical climates. We have seen, in note 15 to Chapter II., an instance of early maturity induced by suitable nutrition.

Note 45, *page* 125. It is known that during the winter frogs eat little and hardly grow at all, nevertheless their eggs are formed during that season. Precisely the same obtains with regard to *Limnæa*; I have proved that the minimum of temperature which allows them to assimilate food and so to grow is much above the winter-temperature at which they deposit their eggs. It is known, moreover, that the larvæ of frogs which have not grown fast enough in the first year to allow of their transformation taking place in due time, live through the winter as tadpoles and do not begin to grow again till the following summer. Now, it would be interesting to investigate whether in larvæ thus retarded by cold the germ-glands are any further developed than is normally the case in the larva stage.

Note 46, *page* 125. According to the result of researches conducted by me during many years, in large individuals of the Axolotl about 48 hours are sufficient to allow of a large number of unfertilised ova to pass from the ovary into the oviduct, to become surrounded with an albuminous envelope, to be fertilised and deposited. I have repeated the experiments which prove this many successive years with the same results. If the Axolotl is kept in small aquaria without plants or sand, individuals that are sexually mature will deposit no ova, even though the water is changed daily and they are well supplied with food.

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I have by this process reduced to sterility for two whole years eight old Axolotls, which had previously produced seven generations of young ones; when I replaced them in a large aquarium with running water, sand, pebbles, and plants, in fifty hours they began to deposit eggs again and produced from 900 to 1,000, of which at least 700 developed. This in no way depends on the season of the year; at least three broods of eggs can be obtained from the same female in one year. But the experiment is apt to be rather a dangerous one, for the males not unfrequently perish if the sexual processes are interrupted too soon.

Note 47, *page* 126. To these larva-forms belongs the much-talked-of Axolotl, whose capability of becoming under certain circumstances a gill-less land-animal—Amblystoma—has been most undeservedly celebrated as a perfectly marvellous phenomenon. It was assumed that in Mexico, its native home, it never underwent any such transformation. But this is incorrect, for in the museum at Vienna there are specimens of Amblystoma and of Axolotl which were collected at the same time in the lake of Mexico. I owe this observation to my friend Steindachner. The Axolotl of Lake Como, by the Central Pacific Railway on the summit of the Rocky Mountains, according to Mr. Carlin, always is transformed into Amblystoma—it is *Amblystoma mavortium*. But the effects of an insufficient body of water, which is said by Weissmann to cause the transformation of the Mexican Axolotl, cannot occasion it in that of the Rocky Mountains, for it takes place in the water; and the Amblystoma, so long as they are little, actually live exclusively in the water, as I know by my own experience. A young Amblystoma, which I kept alive for a long time, never went out of the water of its own free will, while one nearly twice as large lives entirely on land and only takes a bath now and then. It always goes into the water when the temperature of the air in the cellar, in which my aquaria stand, falls below that of the water—down to about 6° or 8° C.

Note 48, *page* 129. Brauer's researches on the Phyllopoda contain a mass of valuable observations on this point, which I will here collect and reproduce for the sake of their wide general interest; unfortunately they cannot be tabulated.

In all the species of Branchipus, *e.g. Chirocephalus Braueri*, which first appear in early spring in pools of snow-water, a rapid rise of temperature from the freezing-point is the first and chief condition of development. These species perish at a temperature of 19°C. At a suitable temperature—about 10°C.?—the development of Chirocephalus from the egg to sexual maturity takes only twelve days.

Freezing the soil acts upon *Apus cancriformis*, *Branchipus stagnalis*, and *B. torvicornis*, in the same way as desiccation, and in warm spring days they develope in snow-water pools just as quickly as at midsummer in warm rain-water pools.

Eggs of *Lepidurus productus* kept in damp earth from April till

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December, and then exposed to freezing for 14 days, at 6° C., yielded a large number of larvæ. The fully developed *Lepidurus productus* can bear a temperature only of from 0° to 18°C.

The eggs of a species of *Apus* from Khartoum, on the other hand, developed in great numbers at 25°C.

Compare on this subject the data given in '*Saison-Dimorphismus*' by Weissmann, as to the accelerated development of different individuals of the same species of caterpillar under a raised temperature.

Note 49, *page* 132. Möbius says: 'Mollusca, Crustacea, and worms which occur in the deepest parts of the Arctic Ocean, are also found in the shallow portions of the Baltic; but they are much larger than those in our milder latitudes, because no extreme changes of temperature there interrupt the quiet order of the vital processes, as they do in our more variable seas.'

Note 50, *page* 133. Mr. Buxton himself has not given any account of the matter. I have taken my information from an interesting paper by Herr E. Friedel, in the *Zoologischen Garten*, 1871, p. 65. In the winter of 1867–68, the cold in Mr. Buxton's wood marked −7° C., and yet not one cockatoo perished. Strangely enough, the Carolina parrot (*Psittacus carolinensis*) suffered most, though in America it is distributed as far as Canada; while the true tropical Cockatoos of the Moluccas throve extremely well. It is to be regretted that this experiment of Mr. Buxton, who is now dead, should not have been still further carried out by his brother.

Note 51, *page* 136. Möbius says: 'We ought not to be surprised at finding eggs of mollusca and of worms in the depths of the Gulf of Kiel at every season of the year, even when it is covered with ice. On January 26, 1862, a stake was pulled out of ice which had been formed eight days, to which clung clusters of the eggs of *Dendronotus arborescens* and *Æolidæ*. Nevertheless, most of our Opisthobranchiata spawn most freely from May to July.' Hence a certain periodicity is displayed in the Gulf of Kiel; and it would seem, according to Möbius, that the young brood is caught in the greatest abundance soon after the time when the deposition of eggs has reached its greatest height, while large specimens are found all the year round.

Note 52, *page* 136. In the Gulf of Kiel the mean monthly temperature varies, at the depth of 16 fathoms, between a maximum of 14° and a minimum of 1·5° C. In the Philippines the difference between the extreme monthly mean of the temperature of the air reaches at the utmost 7°. In the Baltic and in England, as remarked by Meyer and Möbius, at the same depth, the water is much less strongly affected by variations in the temperature of the air. To what depth these variations do in general affect our seas is not known, and it must at any rate be greatly influenced by local conditions.

Note 53, *page* 136. The largest number of *Aspidochirotæ* in th

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Philippines live in 0° F.; in the Mediterranean, in 20–30° F.; in the North Atlantic, in 30–60° F.

The largest number of *Dendrochirotæ* in the Philippines live in 1–10° F.; in the Mediterranean, in 10° F.; in the North Atlantic, in 20–60° F.

The largest number of *Synaptidæ* in the Philippines live in 0° F.; in the Mediterranean, in 1–10° F.; in the North Atlantic, in 1–10° F.

Brachiopoda—*Lingula*—which occur only at great depths in the North Sea, in tropical seas are found near the surface, and even sometimes exposed to the ebb and flow of the tide.

Note 54, *page* 137. If we assume that the place where we find the greatest number of individual species and genera living together is to be regarded as their primary habitat—or centre of distribution—then the Crinoids, Sponges, and many other remarkable forms now living at the bottom of the sea must decidedly be designated as cold-water animals. For by far the larger number of them live at depths where the temperature remains without any conspicuous variation throughout the year at the low point of from 1–2°C.

Note 55, *page* 139. Schmankewitsch's observations on Artemia and Branchipus promise to be of the highest interest in this respect. He found that in individuals which had their assimilation interfered with by a too considerable increase or diminution of the saline components of the water, the injurious effects of this saltness could be entirely neutralised by a diminution or, on the other hand, by an increase of temperature. He furthermore observed that the size of the gill-sacs of Artemia was directly dependent on the temperature of the water, increasing in size with a higher degree of warmth. However, he detracted from the value of his observations by introducing into his estimates one wholly unknown quantity, namely, the amount of air contained in the water (in his experiments), and by attempting to explain everything by the variable proportion of air contained in water of different salinity at different temperatures. General propositions, such as he puts forward hypothetically as to the part played by the air contained in the water, are in such a case of no use, or even misleading.

CHAPTER V.

Note 56, *page* 146. It was impossible to enumerate in the text all the fresh-water animals that live in salt water; I here subjoin a tolerably complete list, which, however, makes no pretension to being absolutely exhaustive.

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Turbellaria.

Microstomum lineare, at Greifswald, in the Baltic (M. S. Schultze, *Arch. f. Naturges.*, 1849, v. 15).

Annelida.

Enchytræus spiculus } Frey and Leuckart, at Heligoland, on the
Sænurus neurosoma } seashore in mud (Frey and Leuckart, *Zur Kenntniss wirbelloser Thiere*).

Tubifex papillosus, Clap.
Heterochæta costata, Clap. } In the Atlantic (Claparède).
Ctenodilus pardalis, Clap.

Pachydrilus, Clap.—All the species live in brine-pools, as Kissingen, Kreuznach, &c.

Pontodrilus Marioni.—Sea-coast near Marseilles, in pure sea-water.

Cystobranchus viridis, Verrill.—A leech, living equally in fresh and salt water (Report of Prof. Baird on Fisheries for 1872–73, p. 686).

Arthropoda.

1. *Crustacea.*

Gammarus, species
Cyclops, species
Cypris
Palæmon Idæ (Heller)
Palæmon, species n.

} Found by me in estuaries which occasionally contain strongly salt water, at Zamboanga, S.W. point of Mindanao, Philippine Islands—October 15, 1859, by my diary. The typical genus Palæmon is a true fresh-water form; almost all the species live in pure fresh water, and many occur high up in mountain streams as far as 6,000 feet above the sea. Only the two species here mentioned occur in brackish water or on the sea-shore. *Palæmon Idæ* I also found in the harbour of Hong Kong.

Astacus.—Two species in the Caspian Sea; associated with marine species (Eichwald, *Arch. für Naturg.*, iv. Jahr.).

Branchipus stagnalis, a typical fresh-water form, is said by Braun to grow much larger in salt than in fresh water, but he does not mention whether the Crustacean remains otherwise unaltered.

Daphnis rectirostris and other species live, according to Schmankewitsch, equally well in salt and fresh water, but they exhibit certain differences depending on the medium.

2. *Arachnida.*—Sea-mites are by no means rare. Gosse has described three English species (*Ann. Nat. Hist.*, ser. 2, vol. xvi. pp. 27, 305).

Pontarchus was found by Philippi on the shore at Naples.

Thalassarachna Verrillii (Pack.) lives in deep water off the American coast (*Silliman's Am. Journ.*, 1871, February). I myself have found

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true spiders in fissures in blocks of coral which were under water at every high tide; they were very common in Bohol and at Zamboanga in the Philippines, but as yet remain undescribed, for my collection of Arachnida is in the Hamburg Museum, and has not been worked upon.

3. *Insecta.*—Darwin, in his well-known *Naturalist's Voyage*, alludes in many places to marine insects, principally beetles and bugs. Many insects have lately been discovered on the coast of North America by Baird (*Rep. on the Condition of the Sea-fisheries of the South Coast of New England*, 1871-2, p. 1) and Packard (*Proc. Essex Inst.* vol. vii. p. 44, and *Silliman's Journal*, 1874, p. 131). These are beetles, bugs, and flies. I found a few marine insects in the Philippine seas, but they unfortunately remain undescribed. Of older observations I may mention Slabber's dipterous larva, probably the larva of a species of *Chironomus*; and I found an abundance of a very similar species in the Philippine seas, where swarms of flies sometimes cover the surface in still bays; then Audouin, who observes that *Blemus fulvescens* surrounds itself, like the fresh-water *Argyroneta*, with a bubble of air. Among the Hemiptera—*Salda*, *Corixa*, *Hygrotrechus*, and *Halobates*—the species of *Halobates* are most conspicuous, for they are found in every stage of development running about on the surface of the sea, often hundreds of miles from land. Eight species of the genus, as I am informed by my friend Dr. Hagen, have been described; that described in the text and discovered by me is a new species and the largest of all. They are found in the Atlantic, Indian, and Pacific Oceans, as well as in the Chinese Sea, but only in tropical or subtropical regions.

Insects are also found in salt-water lakes inland. Packard found eight different species in Clear Lake (*Silliman's Journal*, 1871) and one in Lake Mono. Numerous insects exist in the brine lakes of Europe, but no collection or complete description of them is known to me. I experimented this year on some larvæ of flies which I found in a basin in the courtyard of the Würzburg University; they lived in sea-water very happily for five or six days, but then perished. I suspect, however—and shall test it more accurately next year—that they died for want of food. Compare with this Plateau's experiment; see below.

Mollusca.—*Cyclas*, *Unio*, and *Anodonta* live in the Livonian Gulf associated with *Tellina* and *Venus*. In the Baltic we find *Limnæa auricularia* and *ovata*, and *Neritina fluviatilis* with marine mollusca.

Paludina and *Neritina* are found in the Caspian with *Mytilus* and *Cardium*, according to Eichwald.

Planorbis glaber (Jeffreys) is found in 1,415 fathoms north of Cape Tenez, Algiers.

Unio sp., within reach of the salt-water flow in Brisbane river; (*Voy. of Rattlesnake*, vol. ii. p. 362). Baer found *Unio* at the mouth of the Dwina.

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Nilsson found an *Anodonta* on the sea-shore in Sweden and Norway.

Neritina viridis in the sea, in 3–10 fathoms, and in estuaries in the West Indies.

Neritina matonia (Risso) at Nice.

There are many brackish and salt water species among the *Neritinæ* and several of them are highly characteristic of their habitat. I myself found not less than 16 or 17 species in the Philippines. In pure salt water (3–4 per cent.) I found *Neritina Mortoniana, pulchella*, and *panaensis* new sp., all belonging to the same group. In brackish water, or in spots bathed by salt and fresh water alternately, were the following: *N. Mortoniana, paradoxa* (new sp., *cassiculum*; then *subauriculata* and four allied species; in the mangrove swamps, *N. communis, ziczac*, and a few other species, and finally, in the same locality, but exclusively on the trees, *N. dubia, cornea*, and *subsulcata*.

Melanopsis costata, in the Dead Sea (Schmarda, *Geog. der Thiere*, i. p. 53).

Rissoa ulvæ, a *Hydrobia*, in slightly salt water or in very salt water.

Vertebrata.

Gasterosteus aculeatus
Anguilla fluviatilis } Gulf of Kiel.

In the brackish water of the Baltic Archipelago, according to Eckström, the following fresh-water fishes are found living:

Cottus gobio, Lota vulgaris, Gasterosteus, Acerina, Lucioperca, and thirteen Cyprinidæ.

Eichwald found the following fishes in the Caspian Sea: *Cyprinus, Esox, Perca, Lucioperca*, and *Cobitis*, associated with true marine species — *Clupea, Syngnathus, Gobius*.

If we regard the Crocodile as a typical fresh-water animal, we must mention here that *Crocodilus biporcatus* of the eastern hemisphere, and an American species, according to Humboldt, live in the sea. *Amblyrhynchus ater* is also a marine reptile.

The mammalia and birds that live in the sea can scarcely be included under this head, and an enumeration of them would be superfluous, as they are very generally known.

Note 57, *page* 146. All sea-snakes are viviparous. The females retire to hollows in the rocks in low islands where the young are born, and they do not immediately abandon them, though it is not known how long they remain with them. I found once on the east coast of Mindanao an enormous female, apparently of *Platurus fasciatus*, lying quietly curled up between limestone cliffs, and among its rings and partly on its body lay at least twenty young ones which already measured, as I should estimate, more than two feet in length. It was by the narrowest chance that in climbing over the cliffs I did not walk into this nest of

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snakes. My foot was raised, and not more than two feet from the spot, when I discovered the venomous brood just below me.

Note 58, *page* 148. The following list of marine creatures living in fresh water is not complete.

Cœlenterata.

Cordylophora lacustris (see text).

Bryozoa.

Membranipora bengalensis (Stoliczka, *Proc. Asiat. Soc. Beng.* July 1878).

Victorella pavida (Kent, *Quart. Journ. Micro. Soc.* 1870).

A *Flustra* of a closely allied species in a fresh-water tank at Nagpoor, on the shells of *Paludina bengalensis* and on water plants (*Ann. Mag. Nat. Hist.*, ser. 3, vol. i. p. 168).

Annelida.

Nereis and *Nemertes* of various kinds were found by Tscherniawsky in a lake in Mingrelia of which the waters are drinkable. *Manayunkya*, a Cephalobranchiate discovered by Leidy in fresh water at Philadelphia.

Arthropoda.

The number living in fresh water is extraordinarily great; I will here mention only the most important, and refer the reader to the great work of Ed. von Martens.

Species of *Balanus* in Lake Palæotoma, according to Tscherniawsky.

Cypris salina and *Cypridopsis aculeata* in quite fresh water, according to Brady (*Nat. Hist. Trans.* Northumberland and Durham, vol. ii. part i. p. 121).

Bopyrus, sp. div.? Besides those in the Philippines (see text) species occur in India; and in various museums, as in Munich, I have seen them with a fresh-water Palæmon, *P. indicus*. To my knowledge they have not yet been described.

A species of *Penella*, according to Peters, lives on a *Gobius* in pure fresh water in the Laguna de Bay at Manilà.

The marine forms which now are found at the bottom of the Swedish and Norwegian lakes are of the highest interest: *Mysis relicta* (Lovén) is still living as *Mysis oculata* in the sea near Greenland; *Pontoporeia affinis* lives in the Baltic and in northern fresh-water lakes. Both species have lately been found by Alleyne, Nicholson, and Smith, in the great North American Lakes Ontario, Superior, and Michigan (see *Silliman's Journ.* ser. 3, vol. v. 1873, p. 387; vol. ii. 1871, pp. 373, 448; vol. vii. 1874, p. 161.

I may add to the list of fresh-water crabs given by Martens *Varuna*

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literata, of which I have found identical specimens on Fucus, on the high seas, in brackish water in the estuaries of the Philippines and in pure fresh water high up the country in Luzon; it also lives in Lake Taal. Three or four still undescribed species of the marine form *Hymenosoma* I discovered in the bogs and rivers of the Philippines and in the river near Canton. *Birgus*, *Cenobita*, many *Grapsoidæ*, *Gecarcinus* and others—Crustaceans living on land—properly speaking do not belong here, but they may be mentioned, for at least they do not live in sea-water and are certainly often enough exposed to rain.

A species of *Penæus* lives in a tributary of the Sutlej at the foot of the Himalayas (Huxley, *Proc. Zool. Soc.* 1878, p. 787). *Penæus brasiliensis* goes high up the rivers of North America. (Baird. *Rep. on Fisheries*, 1872.)

Mollusca.

No marine mollusca living in fresh water, besides those named in the text, are known to me; perhaps, however, *Teredo senegalensis* (Blainv.) may be added. Aucapitaine's statement, that *Cypræa moneta* is found in the waters of the interior of Sudan and caught by the natives with calf's hides, has been disputed, but Aucapitaine repeatedly maintained the truth of his assertion. It does not appear, however, to have been confirmed by later travellers.

Vertebrata.

Many migratory marine fishes might be added to the list given in the text; for instance, the species of Shad, many *Pleuronectes* and allied forms—a flounder occurs as high up as Metz and Trèves (Trier) according to Leuthner. Cat-fish and the well-known Manatus live in the rivers of S. America (the Indian sea-cow—Halicore—the nearest ally of the Manatus—is found only in the sea) with numerous other fishes whose nearest congeners are typically marine, such as a species of *Diodon*. In the eastern hemisphere several species of the genus *Hemirhamphus* live in fresh water which are only specifically distinct from their marine allies.

Note 59, *page* 151. According to Bernard's researches on the frog and Plateau's on Crustacea, we might almost be tempted to suppose that in all animals that migrate from the sea to rivers, and *vice versâ*, the different degree of saltness between their tissues and the surrounding water would be rapidly equalised by the osmotic action of the skin. In many creatures, as, *e.g.*, the Stickleback, this is no doubt the case—though no conclusive experiments have been made even on this fish; in others, as the Crocodile, it may be doubted whether even in individuals actually living in the sea the flesh would be salt. No exact investigations exist. From the easily observed fact that a fresh-water stickleback when suddenly transferred to salt water cannot at first

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swim at the bottom of the aquarium, on account of its relative lightness, and that, by degrees, it acquires the power of doing so, it has been inferred that this acquired power is dependent on the impregnation of its tissues by the salt water. This, however, has not been proved, and there is another way by which the fish may be able to alter its specific gravity—by the reabsorption of the air contained in its air-bladder and constantly renewed in it. In highly aerated fresh water so much air is deposited in this air-bladder and in the vessels generally, that the fish is rendered lighter than the water, and cannot go to the bottom even in fresh water. In my aquaria I have seen Sticklebacks, Bleak, and Axolotl perish from the superabundance of air in their tissues in consequence of the constant addition of highly aerated water. On the other hand, a diminution of the air contained in the air-bladder might, of course, easily occur, and thus the specific gravity of the animal would be raised while the whole volume of its body remained the same.

Note 60, *page* 154. As Beudant's small work is not easily accessible, I shall present the reader with an epitome of his tables on the next page.

It must, however, be observed that in this inquiry no regard is paid to temperature. Now, since, under variations of temperature, the respiratory requirements of the cold-blooded animals are extremely different, we may be allowed to assume that a due regard to this circumstance would have led to somewhat different results from the same experiments.

Note 61, *page* 154. At four miles east of Kiel there is a fossil oyster-bed. 'Thousands of years after the oyster-bed of Waterneversdorf had become dry land, oysters lived in such numbers on the coasts of the Danish islands that they were used for food by man of the "stone age" in this region.' Möbius is inclined to attribute the failure of the oyster in the Baltic to its low degree of saltness, combined with the long duration of a low winter temperature, and the absence of any regular movement of the sea by the tide; he assigns the same reasons for the absence of the lobster, the large crab, *Platycarcinus pagurus*, and the edible sea-urchin, *Echinus esculentus*.

Note 62, *page* 155. Prof. Verrill, of Yale Coll., U.S., one of the most accurate students of the American Crustacea, in a conversation I had with him on this subject, disputed the accuracy of this estimate of Schmankewitsch. He said: 'The only characters which can be relied upon for distinguishing the genera Branchipus and Artemia are the male prehensile organs, and these have been entirely overlooked by Schmankewitsch.' I have neither time nor materials at my disposal for a close investigation of this point, and I will only observe that in his latest work he does take the prehensile antennæ of the male into consideration.

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Experiments with fresh-water Mollusca						*Experiments with marine Mollusca*				
Names of species	Number in the first instance, on May 1	Number on July 15		Number on October 15		Names of species	Number in the first instance, on January 1	Number on June 1		Number on September 15	
		In fresh water	In salt water of 2%	In fresh water	In salt water of 4%, after 17 days			In sea water	In half fresh water	In sea water	In quite fresh water, after 15 days
Limnæa stagnalis	30	21	23	16	13	Patella vulgata	30	23	21	16	15
„ auricularia	30	19	17	14	11	Turbo neritoides	50	39	37	22	25
„ palustris	50	33	27	22	19	Purpura lapillus	30	28	26	19	17
Physa fontinalis	50	28	27	17	21	Arca barbata	30	23	22	17	18
Planorbis corneus	30	22	19	15	13	Venus maculata	30	26	23	18	15
„ carinatus	50	34	31	19	16	Cardium edule	30	25	21	17	15
„ vortex	50	37	39	26	22	Ostrea edulis	15	15	13	14	11
Ancylus lacustris	50	39	33	28	25	Mytilus edulis	30	30	30	30	30
Paludina vivipara	30	23	24	21	11	Balanus striatus	21	19	21	18	19
„ tentaculata	50	38	35	31	17	Fissurella uncibosa	30	21	18	14	—
„ obtusa	60	42	39	37	30	Haliotis tuberculata	15	13	11	5	—
Neritina fluviatilis	50	37	31	26	9	Buccinum undatum	20	17	13	11	—
Unio pictorum	20	17	13	8	—	Tellina incarnata	30	24	21	13	—
Anodonta cygnea	15	11	10	7	—	Pecten varius	20	19	7	11	—
Cyclas cornea	40	32	25	18	—	Chama lazarus	10	9	5	3	—

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Note 63, *page* 159. It is quite evident that, in point of fact, a modification of the animal does not always result from a change from fresh to salt water, and *vice versâ*, since migratory fishes exhibit no effects from the change of medium. Here it might, no doubt, be said that these changes have not time to take effect, being too rapid. But there are animals which occur simultaneously in fresh, brackish, and salt water, and yet exhibit no differences, while other species display widely divergent forms according to their habitat. To the former belong *Crocodilus biporcatus*, *Varuna literata*, and others; to the latter *Neritina Mortoniana*, which in the sea is smooth, but which in brackish or fresh water often developes spines, the distinguishing mark of the sub-genus *Clithon*, which is characteristic of fresh-water streams.

Note 64, *page* 159. The remark that only small animals occur in a small area is an old one, but not altogether accurate. The saying is familiar that the largest mammals occur only on continents. Even man is to a certain extent subject to this law. Seafaring men, who pass the greatest part of their lives, from their youth up, confined in an extremely narrow space, are generally small, often below the middle height; but it may, at any rate, be questioned whether their small stature is a result of this mode of life, or not rather of the nutrition, the lack of air, hard labour, &c. In other cases, as those of land mollusca, insects, land-vertebrata, and others, of which the same observations have been made, it seems scarcely credible that their small size should be attributable to the direct influence of a narrow area and to nothing else. Thus, for instance, the fact that only small land-animals occur on small islands of recent origin is easily explicable; for as each of these has received its fauna from beyond seas, the smallest animals have most easily reached them, being the most easily transportable, while many large species must be wholly excluded. All investigations on this question of the influence of area ought at any rate to begin with fresh-water animals, since in these the combined causes exhibit the least diversity.

Note 65, *page* 163. The fact is not new. Mr. Jabez Hogg observed it long ago, but he arrived at no general results from experiments, and even his incidental observations are not particularly satisfactorily set before us. (See *Journal of the Microscopical Society*, vol. ii. 1854, 'Transactions,' p. 91.) Blanchard's observations are neither useful nor of general interest.

Note 66, *page* 166. In order not to occupy too much space in my text, I have forborne from mentioning many details of my experiments; but a full report of them will be found in my treatise, *Ueber die Wachsthumsbedingungen der Limnæus stagnalis* (in *Arb. aus dem Zool.-Zoot. Inst.*, Würzburg, 1874, vol. i.). So far as I can detect, every objection is met by the facts there detailed; some even are fully discussed, particularly one not mentioned above—that the relative proportion of the surface of the water to its volume may affect the growth, because the

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amount of air absorbed depends upon it. This objection is positively refuted by experiment, and I have given the figures, which prove that it is quite immaterial whether the surface of the water exposed to the air is large or small; and in the same way the variety of forms and sizes in the vessels employed in the experiments sets aside the idea that the lateral pressure could have any appreciable effect.

Note 67, *page* 167. This seems to have been the case with the Asellus reared by me in an hermetically closed aquarium (see p. 160).

Note 68, *page* 167. In view of the obscurity which prevails on this point, I think it advisable to appeal to a physiologist of acknowledged repute. Paul Bert says in his *Leçons sur la Physiologie comparée de la Respiration*, word for word, as follows: 'La question de savoir à quel organe il convient d'attribuer . . . la fonction respiratoire est souvent débattue avec une insistance pour le moins inutile. Toute membrane animale étant susceptible de dissoudre l'oxygène et, par suite, de se laisser traverser par lui, il est évident que la surface extérieure du corps est, tout entière, une surface respiratoire, et que toute surface intérieure, comme le tube digestif, peut et doit être elle-même, si le milieu oxygéné s'y introduit, une surface respiratoire.' ('The question to which organ we should attribute the function of respiration is often discussed with a persistency which, to say the least, is useless. Every animal membrane is capable of dissolving oxygen, consequently of being penetrated by it; so it is evident that the whole external surface of the body is a respiratory surface, and that any internal surface, as, for instance, the digestive canal, can and must also be a respiratory surface, if the oxygenated medium can but reach it.') We naturally designate as an 'organ of respiration' in the stricter sense, one which by its laminated or foliated structure and highly developed vascular tissue appears to be specially qualified for the function of respiration.

Note 69, *page* 167. All animals living in water are not characterised by a soft skin—for instance, crocodiles, turtles, many snakes, the whale, many insects, &c. In all these respiration is effected by vessels fitted for the passage of air, by lungs in the vertebrata, and by tracheæ in insects. But among these last, when gills do occur, as is the case with many larvæ, the membrane which covers them is extremely thin, and easily penetrable by the air.

Note 70, *page* 171. These mantle-gills of *Lucina philippinensis* have not been hitherto described, and are figured for the first time in the text. They are large tufts which form two pairs situated on the surface of a membrane which begins at the anterior adductor and traverses the pallial cavity, and which has in its posterior part a narrow slit for the passage of the very long and slender foot. These tufts of mantle gills are during life very large; they contain, internally, an extremely developed vascular network; the vessels unite at the root of the gills to form a large trunk, which passes, without becoming confounded with

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the gill-veins, directly into the ventricle of the heart. The other species of this genus are not endowed with these mantle-gills.

Note 71, *page* 171. Besides the two modes of respiration proved by experiment to exist in water-animals (by the outer skin or by the intestine), yet a third mode of respiration seems sometimes to occur. In all mollusca, beyond a doubt, a certain amount of water is taken up into the body and actually into the blood; this certainly serves to dilate the tissues—*e.g.* in the foot—but it is probably useful also for respiration. But this is at present merely an assumption, founded on no exact experiments. The ways in which water, whether fresh or salt, is said to penetrate to the blood are twofold. Many authors assert that it takes place through the pores and the margin of the mantle; others say that it must first pass through the renal organs, which are never absent from mollusca. After carefully weighing all the treatises on the subject, even the most recent labours of Griesbach, I must declare that neither the one nor the other is absolutely proved; the second hypothesis, however, seems to me, judging too from my own investigations, to be the more probable. Both perhaps may be correct, but here, as in all physiological questions, experiment can alone supply the answer.

Note 72, *page* 172. Comparing an eel with a gudgeon of equal weight, the cylindrical form of the eel giving it a much greater extent of surface, the gudgeon consumes in the same time—three hours—on an average 13·8, and the eel only 7·4 of oxygen (see Bert, *Leçons sur la Physiologie comparée de la Respiration*, 1870). His critical observations on the popular, but erroneous, hypothesis that fishes which are tenacious of life, as the eel, can live for a long time on land because their gills are kept free by means of the water contained in the gill-sac, are well worthy of attention.

Note 73, *page* 172. Many important observations have been made as to the interesting phenomenon of intestinal respiration in *Cobitis fossilis*. This fish swallows the air, taking it in through its mouth, and it is deprived of a portion of its oxygen in the intestine. Many other fishes, however, do the same, as species of *Cyprinus* (see Note 75 below). Jobert has recently shown that various Brazilian fishes breathe in the same way as the Cobitis, and even have in the intestine certain processes or folds of the mucous membrane which seem especially adapted to that end; these are species of the genera *Callichthys* (Siluridæ), *Doras*, and *Hypostomus*. We might almost venture to ask whether the *Cyprinidæ* of European waters, when they take in air through the mouth, do not send only a portion of it through the gills and truly swallow the remainder, so as to keep the mucous membrane of the intestine directly supplied with oxygen. If we prevent the species of *Leuciscus* from coming to the surface of an aquarium by placing a wire net just below the surface of the water, so that they

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cannot gulp the air, they soon die, even when an ample supply of highly aerated water is constantly added; frogs, on the contrary, it is almost impossible to kill in this way. This, however, depends to a great extent on the temperature. The lower the temperature the greater is the fish's power of resistance.

Note 74, *page* 173. Bert's experiments were extremely interesting. He proved that at a temperature varying between 0° and 13° C. the oxygen held in the water sufficed frogs for a considerable time, for they need but little. At 19° C. (water temperature) a frog died in 36 hours when enclosed in a bladder which contained almost five litres (less than five quarts) of water; the frog had absorbed all the oxygen contained in the water, as was proved by analysis. This shows that at 19° C. the requirements of the frog are very high. The Axolotl (*Siredon mexicanus*) can endure not merely the excision of the gills but even the complete removal of its lungs, so that in this animal, as in the frog, respiration by lungs and gills can be perfectly replaced by respiration through the skin. I will also observe, incidentally, that it does not appear to me to be clearly proved that those Amphibia which are provided with both lungs and branchiæ—as *Siredon*, *Menobranchus*, *Menopoma*, &c.—do actually breathe through their lungs; *i.e.* that the air they gulp in through their mouth is distributed to the lungs. The anatomical structure of the glottis does not seem to me particularly to support this assumption. May not their lungs correspond physiologically rather to the air-bladders of fishes? (See Note 75.)

Note 75, *page* 173. Since the publication in 1857 of Milne-Edwards's great work, which treats of the processes and organs of respiration in animals, some newer and not unimportant works have appeared. Emery suggests the question whether Amphibia may not store up oxygen in their lungs, as it has been demonstrated that fishes do in their air-bladders. Gréhant shows that a fish absorbs the oxygen normally existing in its air-bladder when it is kept in water of the temperature of the air. Moreau asserts that the amount of oxygen contained in the air-bladder increases with an increase of the action of the air-bladder; a tench, in which he tied up the air-passage leading to the air-bladder, at the end of a fortnight had in it more than the normal proportion of oxygen. Dividing the sympathetic nerve causes the amount of oxygen deposited in the air-bladder to augment continually. Puncturing the air-bladder occasions at first an increased deposition of oxygen. The researches of Gouriet confirm these statements of Moreau; they were, however, instituted rather with the object of detecting the value of the air-bladder as determining the swimming motions of the fish. In a few cases the air-bladder of fishes seems actually to exercise the function of lungs. Mr. Burt G. Wilder (*Proc. Amer. Ass. Adv. Sc.* 1875) showed that it is very probable that the spongy air-bladder of *Amia calva* and of *Lepidosteus osseus* acts as true lungs, and he has

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recently published a further treatise on the same subject. Jobert has lately shown that the spongy air-bladders of *Sudis gigas*, *Erythinus tæniatus*, and *E. brasiliensis*, actually take up air; and the distribution of the vessels in these fishes as well as in *Amia* and *Lepidosteus* is such as we generally find in true lungs. In these instances, according to Jobert's experiments, tying up the air-passage by which the gullet communicates with the air-bladder, and by which apparently the air is introduced, was speedily followed by death.

Note 76, *page* 173. Besides the Rotatoria, Tardigrada, the Anguillulidæ in mosses and a few little-studied Worms, the following Crustaceans have hitherto become known, of which the ova can endure desiccation without suffering the smallest injury: Apus, Branchipus, Artemia, Cypris, Cypridina, Daphnia, Limnadia, Estheria, and many Copepoda. How long the eggs may generally lie dry without perishing is at present unknown. To the data given in the text I may here add the following which I owe to the kindness of Professor von Siebold of Munich. Mud containing *Artemia*, collected in 1872 by Professor Zittel in the oasis of Dahel (or Dahleh?), produced several broods in the beginning of May 1877, but none in the previous years. Mud out of a ditch at Ingolstadt, collected in 1871, produced a quantity of *Estheria* in the winter of 1876. Mud containing *Branchipus* produced a Nauplius in 1877 after lying dry for ten years. The ova of *Lepidurus productus*, singularly enough, cannot endure desiccation.

Note 77, *page* 175. Brauer has studied this subject. Eggs of *Branchipus* (*Chirocephalus*) *diaphanus* developed after a long time, four to seven months, even without having been kept dry; and those of the marine species of *Artemia* also dispense with drying. But for other species of *Branchipus* and for many species of *Apus*, according to Brauer, desiccation is an indispensable condition for the development of the egg.

Note 78, *page* 175. The geographical distribution of the species of *Apus* and *Branchipus*, for instance, offers many singularities. The eggs are minute and can certainly be easily transported by a high wind to a great distance, and even more easily by migratory birds, such as ducks, snipe, &c. We should therefore suppose that both these genera would have a wide geographical distribution like *Cypris* and *Daphnia*, of which I found several species in tropical countries extremely like those of the European continent, though perhaps specifically distinct. But so far as I have sought for Apus and Branchipus in fresh water I have found none either in the Philippines or in the Pelew Islands in the Pacific. Godefroy's catalogue mentions no species of these genera as coming from the tropical islands of Polynesia, and I find none mentioned as belonging to South America, Central America, or India. This may perhaps be attributed to the fact that circumstances have not been favourable to travellers; it is well known that we may often seek in

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vain, for years, for Apus in spots where it had previously been found in swarms. The best method of filling up this gap in our knowledge will be the transmission of mud, with exact information as to the place where it was collected, to scientific experts, as to Professor Von Siebold at Munich or Professor Brauer at Vienna; and by this means the amount of material in the form of animals for investigation will also be increased in a considerable and very desirable degree.

CHAPTER VI.

Note 79, *page* 178. It was Leydig, the founder of all truly scientific —that is to say comparative—histology, who first pointed out that excessively fine ramifications from the tracheæ traverse every portion of the body of insects and lie between all their constituent parts. He showed that even in the eye, in the ganglia of the brain, and in many glands, &c., tracheæ are to be found between the cells of the organs, that they constantly lie quite close to them and not unfrequently end in a peculiar manner. Thus Leydig first discovered the vesicular ends of the tracheæ among the constituent parts of the dioptric apparatus of the fly, in the crystalline spheres. Even the cells of the fatty tissue —on the presence of which the survival of many insect-larvæ through the winter seems to depend—are in direct connection with the tips of the tracheæ.

Note 80, *page* 179. From what is stated in the text it might seem to follow that the distinction between arterial and venous blood cannot exist in Insects, which breathe by tracheæ, since by that mode of respiration the air is distributed to every part, and consequently the afferent and efferent vessels may contain blood which in each is equally rich in oxygen. It must not, however, be forgotten that even in Mammalia the difference between the two kinds of blood—the highly oxygenated arterial blood and the poorly oxygenated venous blood—is essentially occasioned solely by the absolute, or relative, localisation of the function of respiration in organs especially fitted for it—the gills and lungs. Thus, if in insects also there should be organs whose sole task it was to extract more oxygen from the tracheæ than other parts could, or—when the respiration is effected by water—could deposit it more abundantly in the tracheæ at one place than another, such arrangements would certainly contribute to make the blood richer in oxygenated particles in such spots than elsewhere; and hence, if we

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could prove such a difference in the degree of oxygenation of the blood in different portions of the insect, we must speak physiologically of arteries and veins. Now this, it would seem, is sometimes the case, as in the external breathing organs of many insect-larvæ living in the water, or in the very curious conical structures at the termination of the intestine of flies, which, on account of their extraordinary development of tracheæ, there is now a very general disposition to regard as intestinal branchiæ. In this last instance certainly it is not very clear how they are to act as organs of respiration, since it is certain that flies do not carry oxygenated water in the end of the intestine, and no observations as to the inhalation of air through it have been made to my knowledge. However, a small difference in the oxygenation of the fluids must, no doubt, exist in different portions of the body even in insects.

Note 81, *page* 181. I will here briefly describe an observation accidentally made, but frequently repeated, which suggests the idea that some animals, and especially Infusoria, may possibly be capable of absorbing (and even assimilating ?) carbonic acid. In infusions prepared with the water procurable at Würzburg, which contains a great deal of lime, an excessively thin film is rapidly formed of carbonate of lime, beneath which various Infusoria crowd in masses. If the water is slightly shaken, the fragments of this film roll up into little cylinders, thus enclosing a minute quantity of air, as may be seen by examination with a microscope; since these can be obtained only from the surface of the water, they must certainly be rich in carbonic acid. If now we transfer these little tubes containing air with some infusoria to a moist chamber, we see that they are not unfrequently consumed by the infusoria, and if we then watch for some length of time one of the specimens which has just fed, we shall soon detect that the air in the lime-tubes disappears, and finally the tubes and the air contained in them are completely absorbed. I have frequently repeated this observation, and have particularly noted whether or no the air might not escape in the form of minute bubbles from the oral opening or be removed in the pellets of food; but this was never the case, and I can most positively assert that all the air was perfectly absorbed. Of course this is not hereby proved; still, though I was not able to carry the observation any further, I regard it as sufficiently interesting to be recorded here. Bert says very decidedly in one of his papers read at the Sorbonne, 'On the Influence of Light on Living Beings:' 'On the other hand, infusoria containing green matter decompose carbonic acid in the same way as vegetable cells.' On what ground of exact experiment this bold assertion is made I do not know.

Note 82, *page* 181. Only an incidental reference is made in the text to those other gaseous constituents of the atmosphere which, like carbonic acid, are endurable in small proportions, but extremely injurious

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in large ones. To these belong all the effluvia of decaying matter, sulphuretted hydrogen, &c. But besides the fact that many insects actually depend on such effluvia for their existence, and many larvæ of insects, though air-breathers, live in putrefying matters, we must conclude that such gases are not universally injurious to all animals alike. Even among the vertebrata the difference in this respect is considerable. I once kept, in Manila, a large sea-snake at least two feet long, in a glass vessel hermetically closed, and three parts full of water; the water in a few days became putrid, but the snake lived for twenty-one days in the pestilential atmosphere of the vessel containing it. It is even a question whether then death ensued from the direct evil effects of the mephitic vapour, or not merely from the lack of oxygen after the absorption of the small portion contained in the creature's lungs, and in the air enclosed in the glass.

The reader can also compare the observations of P. Bert, *Physiologie comparée de la Respiration*, with those of Milne-Edwards, *Leçons d'Anatomie et de Physiologie comparée*.

Note 83, *page* 184. The view is sometimes put forward that certain stripes running parallel to the mouth of univalve shells—of the Helicidæ, for instance—afford an indication as to the age of the animal, each stripe being supposed to correspond to a year's growth (like the annual rings in a tree). This may perhaps—but only perhaps—be true with regard to our northern forms; but even among the land-snails of the Mediterranean, it ceases to have any application. I myself saw that in Spain and the Balearic Islands, after a summer's rest of about two months, or even more, almost all the species began to couple, to lay eggs, and to grow again as soon as the autumn rains fell in September. Now, as the eggs of land-snails develope very rapidly, and never remain, like those of many insects, undeveloped through the winter, the young must be hatched out in the autumn; their growth is probably interrupted during the winter, as is, in fact, not unfrequently indicated by the presence of a stripe. They begin growing again in the spring, and apparently deposit their first eggs before the summer drought comes on; after their summer rest they lay eggs a second time, but nevertheless continue to grow, and thus form a second line of growth. This, at least, would seem to be the inference from the fact that in the autumn, along with the fully grown specimens, small ones are to be found with only one stripe, and which seem to have been hatched out in the spring. So far as I know, no attention has hitherto been paid to this circumstance.

Note 84, *page* 186. Planarian worms are worms of low type and simple structure, for the most part flat, living chiefly in the water; in the sea they often attain a considerable size, and exhibit the most brilliant hues. The first discovery of a land Planarian was made by the well-known Danish zoologist, O. F. Müller, but his remarks on *Planaria terrestris* excited little attention till Darwin published his observations

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on the land Planarians of South America. Since then these animals have been examined anatomically, particularly by Schultze, Metschnikoff, and Moseley, and we are acquainted with a great number of such forms through the efforts of travelling naturalists (Schmarda, Moseley, F. Müller, and others). It may be stated that they are generally tropical animals, though three species have already been discovered in Europe; here they live only in damp soil, under stones, while in tropical regions they take long walks in the early morning, on trees, rocks, and houses. I found most of those that I collected in the Philippine and Pelew Islands—about 12 or 14 species—in such situations, and among them a few of really colossal size. Of the genus *Bipalium*, represented in fig. 53, I have one species which attains the enormous length of four inches. A complete list of all the land Planarians hitherto described is to be found in H. Moseley's 'Notes on the Structure of several Forms of Land Planarians, with a Description of Two New Genera, &c.' (*Quart. Journ. Mic. Sci.*, new ser., vol. xvii.).

Note 85, *page* 187. Nemertidæ are also for the most part water worms, moving in the water by means of the microscopic cilia on their skin. They are systematically allied to the Planarians, but distinguished from them externally by their perfectly circular, elongated form, and particularly by a proboscis opening at the fore end, which is wanting in the Planarians.

Note 86, *page* 188. This Balearic species seems to be *Talitrus platycheles*, Guérin. I have seen species of true Orchestia, both in the Pelew Islands and in the Philippines, where they live far from water, under stones and brushwood, in damp woods.

Note 87, *page* 188. The arboreal Neritinæ usually live in mangrove swamps, high up on trees. I never saw them in the water, but they deposit their eggs on the surface of water, so that they are, at any rate occasionally, touched or covered by brackish water. I found the following species in the Philippines: *Neritina dubia, communis, cornea, subsulcata, zic-zac, Cumingiana, plumbea*, and a few new and undescribed species.

Note 88, *page* 189. Günther divides these fishes into the following families: Luciocephalidæ, Labyrinthici, and Ophiocephalidæ. Of these the first two have both the secondary cavities of the branchial cavities furnished with convoluted labyrinthine folds; the species of the third family have only simple secondary cavities with feebly developed folds, or none. The species of *Saccobranchus*, allied to the Shad, and *Amphipnous cuchia*, an eel-like form, allied to the Symbranchidæ, have also a subsidiary sac to the branchial cavity, but without any folds.

Note 89, *page* 190. The observations of Sir Francis Day are to be found in the *Proc. Zool. Soc.*, London, 1868, Part II. p. 274.

Note 90, *page* 192. I have, in the Philippines, frequently had the opportunity of observing these creatures alive, and I can assert decidedly

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—what, to my knowledge, other travellers had already described—that the Ampullariæ breathe not merely with both gills and lungs, but that they do so in regular alternation; for a certain time they inhale the air at the surface of the water, forming a hollow elongated tube by incurving the margin of the mantle, so that the hollow surface is enclosed against the water, and open only at the top. When they have thus sucked in a sufficient quantity of air, they reverse the margin of the mantle, opening the tube into which the water streams. The changes are tolerably frequent, once or twice in a few minutes, depending, probably, on the temperature. No physiological explanation of these hythmic alternations can, however, be at present assigned.

Note 91, *page* 192. Fritz Müller, the well-known naturalist in Brazil, in his admirable essay, *Facts and Arguments for Darwin*, has given us a quantity of observations on the mode and way in which crabs breathe air. The modes by which this is accomplished are very various; and even the structural relations implicated in the process, which are sometimes extremely peculiar, irresistibly prove that the different air-breathing Crustaceans no more constitute a natural family than do the Labyrinthici among fishes.

Note 92, *page* 193. In a few works, distinguished for their dogmatic style, and intended for the use of students in medicine, it is stated that these land-crabs, and above all *Birgus latro*, breathe no air, but only water, and that the branchiæ are exclusively the organs of respiration. I cannot understand how so incorrect a statement can have become so common, for the authors of these works cannot adduce a single experiment which proves that in fact the introduction of oxygen into the blood takes place exclusively by means of water, and through the branchiæ. Since absolutely no physiological experiments exist on this subject, this erroneous view can only rest on an interpretation—which is acknowledged to be insufficient—of the morphological features. So far as here regards *Birgus latro*, I have shown in the text, and in the cut on page 5, that the views hitherto entertained as to the structure of the branchial lungs of this animal are altogether false, and that every morphological attribute is to be found in them which we should expect to find in a true lung.

Note 93, *page* 195. I have before alluded to the injury that may sometimes result from a superabundance of air in water, by which so large a supply may be taken in by a fish (a stickleback or an Axolotl) that it may become lighter than the water and so unable to find its food at the bottom.

Note 94, *page* 198. Dr. August Pauly. With regard to the last point alluded to in the text I must be allowed to make a few notes. Pauly says that Limnææ, when they are kept under water and have no opportunity of inhaling air-bubbles into their lungs, keep the lungs closed. A mollusc, having its lungs filled with air, will absorb

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the oxygen contained in that air if it is kept under water, and instead of it carbonic acid will be deposited in the lungs. This gas, being positively injurious to the creature, must presently be expelled, and consequently the lungs must soon become empty and so collapse, or they must be replenished with air or water. In Pauly's experiments the former was the case; he expressly says the lung-cavity was empty, 'as could be seen by its shrunken aspect from outside.' But he conducted the experiment in a somewhat energetic fashion. He forced the animal to expel all the air from its lung-cavity under water. Now, he himself says that the expulsion of the air in consequence of irritation may sometimes even occasion the death of the animal; hence the question is allowable whether the persistent closing of the lung may not have been a diseased result of the irritation in itself so unendurable. The experiment must be repeated in some way differing from Pauly's before it can be regarded as perfectly conclusive evidence of the inferences given above in the text.

CHAPTER VII.

Note 95, *page* 203. Some mollusca, as Patella and Navicella, are immoveably attached to the rock for the whole period of their existence; they never quit one spot, and not unfrequently make a more or less conspicuous impression in the stone. How? This is not known.

When they are not disturbed, they usually lift the fore-part of the shell just so much as is requisite to admit a fresh supply of water to the branchial cavity, and of food to the mouth. If they are touched they shrink back, and the shell adheres so closely to the stone that it is impossible to loosen it from its hold without injuring it. I have often endeavoured to loosen a Navicella hardly an inch in length from its situation on a stone in a swift mountain torrent, by lateral pressure on the shell, not by insinuating a knife under it; but I most rarely succeeded—never, indeed, unless I took the creature by surprise; if it were in any way on the alert, I could not do it but by application of the knife, and a consequent injury to the shell. The case is the same with Patella (limpet), and many other mollusca; even the creeping kinds, as Chiton, can adhere uncommonly tightly by suction, and in every case the foot is the organ employed.

Note 96, *page* 205. A few deep-water Siphonophora have lately been described by Studer. Two species were dredged up from a depth of from 800 to 1,000 fathoms, belonging to the genus *Rhizophysa*, which,

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like many others, has an air-bladder at the upper end of the sac. The air-bladder has an opening at the top by means of which, when the creatures are kept in small vessels, the air easily escapes. I am astonished to find that Studer does not seem to have particularly remarked this feature—and yet it seemed to offer so obvious a parallel with the fishes living at great depths, and provided with air-bladders! In these, as has long been known, the air contained in the bladders is exposed to very considerable pressure; if this is suddenly removed by the fish being rapidly brought to the surface, the air, previously compressed, expands and distends the belly; a prick allows the air to escape, the air-bladder collapses, and the fish, restored to its natural size, can swim again. It is evident that the air in the deep-sea Rhizophysæ must also be much compressed, but in them the perforation already exists by which it can escape when the animal is raised to the surface, and the expanding air threatens to burst the bladder. Studer says nothing about this very conspicuous expansion of the bladder, and we may therefore suppose that the Rhizophysæ had parted with the chief portion of their air before reaching the surface. This filling and emptying of the air-bladder, which must undoubtedly exist in the Rhizophysæ to enable them to rise or sink, recalls the hydrostatic vacuoles of the Arcellidæ.

Note 97, *page* 205. Limnæa and Planorbis are frequently to be seen with the sole—so to speak—of the foot spread out on the upper surface of the water, and thus swimming in an inverted position; but this swimming is more accurately described as creeping on the *under surface* of the air, the plane of contact of the air and water. At first we are inclined to imagine that the adhesion of the foot to this surface is strong enough to bear the whole weight of the animal and its shell. This, however, is not the case; for if the snail is induced to retract its foot so slowly that no air-bubbles are expelled from the branchial orifice during the process, the animal turns over in the water, but it remains floating at the surface, so that at that moment its specific gravity must be less than that of water.

Note 98, *page* 207. It may, perhaps, surprise many readers to hear of the fins of birds. But most water-birds do in fact use their wings for swimming in the water quite as well as for flying in the air. The wings of ducks, divers, cormorants, &c., are not the less true wings. In the penguins, however, the same limbs, morphologically speaking, have become true fins, which the creature can use in the water, but can no longer use in the air as wings. In them, although the portions of the skeleton still correspond in all essentials with those of a true wing, there is absolutely no external resemblance to the true wings of other birds. Anyone may convince himself of this in a zoological collection.

Note 99, *page* 209. This assertion is founded on a careful anatomical investigation of a good many different species—at least six—of the genus Navicella. Naturally there are visible differences between it and

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Neritina, otherwise the two groups would long since have been united in one genus. But the differences in their structure, irrespective of the form of the shell and the structure and situation of the operculum, are so trifling that we are justified in regarding the Navicella as a modified form of Neritina.

Note 100, *page* 212. It is in accordance with this view that we find great variability in the forms of the operculum of Navicella. We know that truly rudimentary organs which have lost their principal function and have not become serviceable for any other well-defined function are, as a rule, remarkably variable. That is the case here. While the opercula of the most dissimilar Neritinæ are of very uniform structure, in those of Navicella we find the widest dissimilarity. My own researches—which certainly are not yet completed—make it seem probable that the deviations from the normal form in a species, even in individuals, may sometimes be very considerable. It is, moreover, a very interesting fact that even the operculum of the male may differ from that of the female.

Note 101, *page* 213. The structure and origin of the shells of mollusca are not, even at the present, thoroughly understood; for although, as to the first point, a vast mass of interesting researches lies before us, no one has yet succeeded by purely histological investigation, and a knowledge, however exact, of the minutest structure of the shell itself, in establishing any fundamental character as common to all shells. At the same time too much attention has been paid to the general relations of the shell when fully developed, and not enough to the development and bearings of those relations. We know, for instance, that in the freshwater mollusca three distinct and very dissimilar layers are to be found. The external layer is a purely organic cuticle; next comes the prismatic layer; and inside this the nacreous layer. It is admitted that the prismatic layer is often wanting. Now, if we are considering merely the details of structure, the correctness of this view cannot be doubted, but it would be quite an error to suppose that every shell in which the prismatic layer was wanting therefore consisted of two layers only, the outer cuticle and the internal nacreous layer. In point of fact, these shells also have three separate layers, and that lying next beneath the organic cuticle differs from a true prismatic layer only by its deviation from it in the physical process of formation; the material composing it does not form distinct prisms as it is secreted. But the spot whence it originates is, on the other hand, an essential character. The organic cuticle and the prismatic layer—the external calcareous layer—are secreted only and invariably at the margin of the mantle; the former frequently between two lobes, or folds of the margin of the mantle, the second from the narrow edge between the margin of the mantle, and a line, not always present, which indicates the insertion of the small muscle of the mantle. From this line as far as to the top of the shell, nothing can be secreted but nacreous material; the growth in thickness

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of the shell, therefore, must depend greatly, or exclusively, on the development of the nacreous layer. It is only when the secreting power of the surface of the mantle is extremely small, while that of the narrow edge which secretes the prismatic layer is unusually strong, that the thickness of the shell can be determined by the growth of the prismatic layer. In such exceptional cases the margin of the shell is always thicker than the main part. Any more minute description of these facts seems to me to be here out of place, and unfortunately I cannot refer the reader to other works, as I have not published anything on the subject, nor am I at present likely to do so.

Note 102, *page* 217. Graeffe says that he has sometimes found a whole family in these galls or cysts. It is not quite clear to me how a family of the Crustaceans could find room in a cavity which is hardly twice the size of the fully-grown *Hapalocarcinus*. It is possible that young larvæ might be found there before their escape, but this is not clearly expressed in the text.

Note 103, *page* 221. This crab, living in *Trachyphyllia*, a West Indian coral, is extremely like *Cryptochirus*, and perhaps belongs to the same genus; this can only be determined by future and more exact examination. But the 'cave dwelling' of this West Indian crab is perfectly unlike that of the Eastern species, which is found from the Red Sea as far as the Pacific Ocean; it is not cylindrical, but has one side quite flat, so that its transverse section is almost exactly a half-circle; the under side of the crab rests against the flat side of the cavity. With regard to the pouch, I have not yet been able to make any investigations.

Note 104, *page* 223. The conditions here described will under some circumstances be available for enabling us to form a much more exact estimate of the rate at which a block of coral grows than has hitherto been possible. The data here given, and presently to be worked out more fully, are certainly hardly to be regarded as the result of perfectly exact investigations; the only really exact observation—carried out, too, in minute detail—is that of Le Conte (in *Silliman's Journal*, series 3, vol. x., 1875), and he found that a coral plateau in Key West (West Indies) exhibited a perfectly regular dependence on the height of the water at different seasons, so that it was always possible to ascertain with great accuracy the rate of growth of the one species of coral observed there—a kind of madrepore—which was about 3½ inches in the year. Now, if the period of growth of a specimen of *Cryptochirus* could be exactly determined, the rate of growth of the coral to which it belonged could also be determined with mathematical accuracy, much more exactly than it could be ascertained by direct measurement of the coral itself. If we assume—what at present, it is true, cannot be proved, though it is not improbable—that the *Cryptochirus* acquires the first six millimètres of its length in the first year, that would give an average

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rate of growth for the massive Astræidæ of 18 feet in a thousand years, whereas Dana allows at the utmost 5 feet. It is not, however, to be supposed that either of these estimates is universally applicable, since the different species of corals, like all other animals, have different rates of growth, and the rapidity might also vary under different circumstances. It would, indeed, be extremely interesting if only the maximum rapidity of growth in individual corals—as those of different reefs—could be established by observation; but to do this would be a highly complicated and difficult task, since the vigour of growth of the animals must depend on a great number of different influences which combine to affect it.

Note 105, *page* 229. I have been at great pains in seeking in books of travels or descriptions of the different species of corals for data as to the various forms which coral-blocks are capable of assuming in different situations, but the results of my search have been terribly meagre. I found, in fact, only the observations made by Ehrenberg to the effect that *Stephanocora Hemprichii*, Ehren., in the Red Sea, forms branched or flattened stocks according to whether it lives in still or in rough water (see Ehren. *Corals of the Red Sea*). This, in my opinion, is the inevitable result of the faulty methods of investigation hitherto applied to these creatures; naturalists are desirous of distinguishing the species, and accordingly they have above everything paid attention to the distinctive character—as with insects, shells, &c.—and at the time—like Dana in his magnificent work on corals, connected with Wilkes's expedition—they have bestowed the utmost pains in ascertaining the limits of variability for individual species, as he has done with the greatest care in regard to certain madrepores. Klunzinger's new work on the corals of the Red Sea supplies an abundance of material of this kind. But up to the present time no systematic observations have been carried out bearing on the question which we are especially studying—as to how far currents in the sea, variations in temperature, or the saline constituents and other physico-chemical influences, may affect each species individually. The excuse to be offered is evidently this: that the fundamental essence of Darwin's theory is only now beginning to exert its influence, and that we are only now beginning to recognise the necessity for not merely putting off these reacting conditions with an attempt at a hypothetical explanation, but for throwing on them the light of carefully conducted research, and, wherever it is possible, of actual experiment. Another and a very serious hindrance lies in the difficulty of obtaining the living material that is indispensable for such investigations; stationary zoologists, qualified to conduct them, are not many in the tropics, and travellers can never have time enough to make any really valuable observations of this kind. We must hope that we may ere long see a few zoological stations established in the tropical seas, such as that inaugurated with

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so much energy and talent at Naples by Dohrn; for it is only in such institutions—which supply, as it seems to me, a real want—that it can be possible to carry on a series of observations through successive years, which is indispensable for clearing up biological questions. Meanwhile let us be thankful that we have that of Dohrn, and a few others recently established, here in Europe. I cannot omit to record my satisfaction that Dohrn has decided henceforth to publish a special journal of his own Transactions, for I am convinced that the Institute itself, as well as zoologists at a distance, who desire information about it, will find it advantageous. The complaint that it constitutes a new scientific journal seems to me ill founded, for such an objection is never raised against a new book, and the work begun and continued in such an institute appears to me to constitute a whole, quite as coherent as the different chapters of a book, or indeed of many monographs, and often of much greater value.

CHAPTER VIII.

Note 106, *page* 259. According to Wiechmann the rocks of the Kokeal formation contained the following fossils:—

Tridacna, Strombus, Mactra, Cyprina, Madrepora, Serpula, Lucina, Tellina, Venus, Spondylus, Fistulana, Balanus.

He regards the eruptive rocks as of tertiary or post-tertiary date.

Note 107, *page* 275. It would be highly advantageous now to criticise the Theory of Subsidence not merely in its application to a particular instance, as I have done, but in its universal bearings, so as to come to some conclusion as to whether my theory of currents, *sit venia verbo*, deserves, or does not deserve, general preference. This, however, is not the place for such a discussion. I will only observe that I believe that, in fact, my theory presents fewer difficulties than the Theory of Subsidence, and may therefore be regarded as more in accordance with nature. On the other hand, I readily concede that sometimes—as, for instance, in the Andaman Islands—an atoll may be formed during a period of subsidence, and yet it may not be exclusively the result of the subsidence. Still, under the assumption that absolutely no influence of the nature above indicated could have formed atolls among the Andamans, this could only have been possible if the subsidence had throughout been slower than the growth of the coral. This appears to be sometimes the case; for the Andamans are said to be sinking at the rate of a foot in a century, while Le Conte gives the maximum growth

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of a coral as one foot in three and a half years, and another observation, in Port Darwin, gives one foot in twelve years. On the other hand, however, there are other islands which prove that the upward growth of corals is certainly never so rapid, and is often remarkably slow. In the Sandwich Islands—which, according to Dana, are sinking—all the corals live at several fathoms below the level of the water, and the case is the same in the Galapagos and the Gulf of Panama. Here, by assuming a subsidence, the growth upwards is less rapid than the rate of subsidence, and it must be even slower, much slower, if we assume an upheaval as going on in these islands. Hence I regard it as quite possible that under certain circumstances a subsidence may be combined with the formation of atolls, and even that it may once have been the sole cause of their formation; but I cannot admit that subsidence is alone sufficient to explain all the conditions and relations of coral-reefs, or even of predominant importance.

The following letter from Mr. Charles Darwin to the author refers to the subject under consideration:—

'October 2, 1879.

'My dear Professor Semper,—I thank you for your extremely kind letter of the 19th and for the proof-sheets. I believe that I understand all, excepting one or two sentences where my imperfect knowledge of German has interfered. This is my sole excuse for the mistake which I made in the second edition of my Coral-book. Your account of the Pelew Islands is a fine addition to our knowledge on coral reefs. I have very little to say on the subject: even if I had formerly read your account and seen your maps, but had known nothing of the proofs of recent elevation, and of your belief that the islands have not since subsided, I have no doubt that I should have considered them as formed during subsidence. But I should have been much troubled in my mind by the sea not being so deep as it usually is round atolls, and by the reef on one side sloping so gradually beneath the sea; for this latter fact, as far as my memory serves me, is a very unusual and almost unparalleled case. I always foresaw that a bank at the proper depth beneath the surface would give rise to a reef which could not be distinguished from an atoll formed during subsidence. I must still adhere to my opinion that the atolls and barrier-reefs in the middle of the Pacific and Indian Oceans indicate subsidence; but I fully agree with you that such cases as that of the Pelew Islands, if of at all frequent occurrence, would make my general conclusions of very little value. Future observers must decide between us. It will be a strange fact if there has not been subsidence of the bed of the great oceans, and if this has not affected the forms of the coral reefs.

'Yours very sincerely,

'CHARLES DARWIN.'

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CHAPTER IX.

Note 108, *page* 284. Zoologists and geologists alike are wont to regard all the land mollusca, or rather their shells, as peculiarly fitted to indicate the affinities and relationship of living and extinct faunas. Now, I do not dispute that they may sometimes be of the greatest utility in this respect, but I must here express my conviction—a conviction derived from years of study of the animals as well as of their shells—that in many cases we have absolutely no right whatever to avail ourselves of the shells of land mollusca for such comparisons; and, moreover, that their classification by the shells, which is universally adopted by conchologists and geologists, and which they have accepted as a natural one, is absolutely and totally worthless and unnatural. Thus every argument based on the assumption that the genera and subgenera as at present distributed are natural divisions, indicating the true affinity of the species they include, must be purely imaginary, a mere castle in the air (such, for example, as *Geotrochus*, *Bulimus*, *Rachis*, *Homorus*, *Hapalus*, *Nanina*, *Leucochroa*, &c., &c.; comp. Wallace, *Geog. Dist. Animals*, ii. 512 et seq.).

Note 109, *page* 287. The careful investigations which I pursued for years, extending over many hundred species, have brought me more and more to the idea that it may be possible to determine the route of migration followed by many genera of land mollusca by a diligent examination of their natural affinities. This evidently cannot be done by an examination of the shells exclusively. These, of course, must not be neglected, but their systematic value has hitherto been greatly overestimated, especially by geologists, and without a close familiarity with the animals themselves we can but very rarely determine the affinities of the species with any certainty. Hence our first task must be to separate those groups of the land mollusca whose shells do, in fact, afford a sure indication of their systematic position from those in which the shell is quite or almost useless for such a purpose. To what a great degree this is often the case is shown by the Philippine genus *Cochlostyla*, of which the shells are so excessively variable—in spite of the similarity of structure in the animals themselves—that no conchologist could possibly describe the genus from the shells. Hitherto we have always had a genus under the name of *Vitrina*, but species were included in it which belong not merely to different genera, but even to different families; these are so much alike as to the shells that, according to that character alone, it was inevitable that they should get classed together. In my work on the land mollusca I have shown that almost all the shells of the Philippines known as *Vitrina* belong to the genus *Helicarion* and the family Zonitidæ, while *Vitrina* is one of

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the Limacidæ. From mere external resemblance a host of shells from India, Persia, &c., have constantly been described as belonging to *Helicarion* which, so far as it has hitherto been possible to investigate the creatures anatomically, all belong to the typical genera of the neighbouring Indian mainland, to which indeed they often exhibit but little similarity even in their shells. The Philippine mollusc *Pfeifferia micans* is often placed under *Vitrina*, and the shell certainly has some likeness to that of *Vitrina*, but the animal is in every particular a true *Cochlostyla* (and thus a true Helix), and is one of the innumerable variations of this variable genus, the structure of the shell completely disguising its true character. If these and the other 200 or so of species of Cochlostyla could be discovered somewhere in a fossil state, geologists would undoubtedly make at least eight distinct genera of them. This instance must here suffice to justify the assertion I have made.

Note 110, *page* 289. Wagner's phrase, which I have somewhat altered in the text, runs as follows: 'Each closed cycle of forms (a species or constant variety) originates in a mechanical process of isolation and colony-formation by individual emigrants from a parent-stock capable of variation; the indispensable conditions of the formation of such a cycle are variability and inheritance. The sum of morphological characters which distinguish it are the result from the sum of differences in the external conditions of life on the one part—such as food, climate, character of the soil—as supplied by the habitat of the isolated colony, when compared with the native province of the old stock, and from the sum of phyletic and individual capacity for variation on the other part as imported by the colonist itself, and transmitted as morphological characters to its progeny and posterity by direct descent. The constancy of the new form always depends on a long-continued period of isolation.'

Note 111, *page* 291. I cannot understand in any other sense the various passages in which Wagner distinctly opposes his theory of 'isolation' to the 'struggle for existence.' I will here quote only one passage: 'The *Achatinellæ* are harmless vegetable-feeders, content with any situation, and their overwhelming multiplication is kept within bounds not by the pursuit of enemies, but by epidemics. They have no vital struggle to carry on for food, since this is supplied in any quantity by the abundant herbage of the soil, nor can we discover that any struggle for propagation can take place among them, since each animal is hermaphrodite, and pairs with any other. If here and there one of these snails, which generally find sufficient shelter by a rapid retreat into their shell, is by chance devoured by a bird or a predatory beetle, or accidentally crushed by a grazing beast, these are purely accidental occurrences, which would be far less likely to reduce their numbers than the constant persecution to which the ladybird for instance, is exposed. Nature has at

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her disposal an all-sufficient means of reducing the too exuberant multiplication of all very fertile species, in epidemic diseases, and no competition is needed or available here.' Now, it seems to me that this sentence can have no other meaning than that I have attributed to it; according to Wagner the 'struggle for existence' means nothing else than a competition between two animals for a certain possession. But is there no struggle for existence when a snail endeavours to escape the causes which produce an epidemic? Epidemics among land-snails are commonly caused by too great moisture or drought; those that cannot escape rapidly enough perish; those that cannot endure drought are destroyed. In an epidemic of rot, or rather of saturation, the old and feeble individuals will perish first; parching heat is least endurable to the young animals, as their shell and diaphragm are not thick enough to protect them against desiccation. Nay, even a direct struggle is not always entirely avoided. In order to escape from drought, many land-mollusca creep into cracks and fissures in the rocks; the first-comers are the best off, for they can creep furthest in, and those that come after close up the opening and prevent the escape of the moisture. Thus, during the dry season in the countries of the Mediterranean, for instance, we find the outer rows of snails almost invariably dead, while any considerable number of living ones are only found at some depth. The conditions are reversed when the rainy season comes on. All the rifts and crevices are filled with water; those lowest down are the first to be immersed, and strive to escape the too abundant supply that soaks their skin; but the dead shells remain attached above them, or those still living, but not yet aroused by the wet, hinder them from creeping out, the water penetrates their pores, and in a few hours they are so 'water-logged' and dropsical as to be incapable of any rapid movement. (It is a great error to suppose that a snail cannot have too much moisture; if one is plunged into water and prevented from escaping within twenty-four hours, it is so completely sodden as to be quite incapable of crawling.) Is not this a struggle for existence? It seems to me that it is a very obstinate struggle for existence when one snail, even after its death, can bar the road to life and freedom to one of its companions. But many of the premisses in the passage above quoted from Wagner are false or quite unfounded. He says that *Achatinella* is one of the very fecund species of which the overwhelming multiplication is more effectually hindered by epidemics than by competition or rivalry. This is either false or devoid of foundation; *Achatinella* is oviparous, and produces only a few young at a time; how often in the year is perfectly unknown. The assertion that every mature hermaphrodite individual is always ready to pair is certainly not proved. It has never been actually disproved by observation that many snails die without pairing from antipathy, though fully grown and mature, and the extraordinary convolutions and gymnastics performed by snails before pairing lead to the conclusion

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that even in these apathetic organisms liking and dislike play a certain part. Whether *Achatinella* is, in fact, spared all struggle in the matter of food, cannot possibly be determined, to judge from the investigations of Gulich. The merely hypothetical superabundance of food is no proof of its real sufficiency; if, for instance, the space where this abundance is supplied is very limited, the animals desirous of feeding will get in each other's way, and it is possible that this might give rise to some quite unknown psychical influence. Many animals, as is well known, eat freely only in solitude. This is very certainly not the case with snails, but they may nevertheless desire a certain amount of elbow-room, a point that has never been observed, or even thought of. But even supposing that these positions of Wagner's were all proved to the utmost extent of their very positive assertions—which is by no means the case —still, the struggle of the *Achatinellæ* against the causes of the epidemics that decimate them is necessarily a competition, though of course not in the same sense as is a duel fought for life or death between two individuals.

Note 112, *page* 292. Notwithstanding that Darwin's works are universally accessible, I will here quote the passages to which I particularly refer. In the first place, with reference to the external conditions of existence, I offer a few extracts: 'Neither migration nor isolation in themselves can do anything. These principles come into play only by bringing organisms into new relations with each other, and in a lesser degree with the surrounding physical conditions' (*Origin of Species*).

'Hence, though it must be admitted that new conditions of existence do sometimes definitely affect organic beings, it may be doubted whether well-marked races have often been produced by the direct action of changed conditions without the aid of selection either by man or nature' (*Animals under Domestication*, ch. xxiii.).

'Such changes are manifestly due not to any one pair, but to all the individuals having been subjected to the same conditions, aided, perhaps, by the principle of reversion' (*Descent of Man*, i. 236). 'Although with our present knowledge we cannot account for the strongly marked differences in colour between the races of man, either through correlation with constitutional peculiarities or through the direct action of climates, yet we must not quite ignore the latter agency, for there is good reason to believe that some inherited effect is thus produced' (*Descent of Man*, i. 245, and on p. 246 he adduces reasons in support of this statement).

One more quotation: 'There can, however, be no doubt that changed conditions induce an almost indefinite amount of fluctuating variability by which the whole organisation is rendered in some degree plastic' (*ibid.* i. p. 113). Compare with this what Darwin says as to the direct external influences which affect the skull (*ibid.* p. 147). But it seems to me to be proved by numerous passages in Darwin's works that he

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regards the principle of isolation of new forms and the hindering of in-breeding with the parent form as an integral portion of his theory. I will here quote the most striking examples. He says (in *Animals under Domestication*, ch. xv): 'The prevention of free crossing and the intentional matching of individual animals are the corner-stone of the breeder's art. No man in his senses would expect to improve or modify a breed in a particular manner or keep an old breed true and distinct unless he separated his animals. The killing of inferior animals in each generation comes to the same thing as their separation.' The struggle for existence combined with other causes produces the isolation which is indispensable to the phenomena of a race or species by causing the necessary separation from the parent form and by hindering its crossing with it again. Elsewhere Darwin says: 'A country having species, genera, and whole families peculiar to it, will be the necessary result of its having been isolated for a long period, sufficient for many series of species to have been created on the type of pre-existing ones.'

Note 113, *page* 293. Günther on the Tortoises of Mauritius and Galapagos, *Ann. Mag. Nat. Hist.* 1874, vol. xiv.; *Silliman's Journal*, 1874, ser. 3, vol. viii. p. 403. These tortoises are also interesting from their enormous size. Günther comes to the conclusion that those of the Mauritius and those of Galapagos must have originated independently.

Note 114, *page* 294. The question whether similar forms can have a polyphyletic origin (be derived, that is, from independent parent stocks) or no, has gradually become the corner-stone of that extreme and dogmatic form of Darwinism which in Germany has been designated as *Haeckelism*.* Haeckel himself, the founder of this creed, allows of no doubt that all those characters collectively of a species or of a genus which present themselves to us as identical can only and unconditionally, as being identical, have been derived from a single parent-stock. This is known as *Monophyletic* descent, and according to this view all the species of a genus must have descended from one parent species, all the genera of a family from one parent genus, and so forth. In opposition to this is the view that a *polyphyletic* origin may be possible, *i.e.* that the forms comprehended by us in a genus or a family may have descended from more than one parent species or genus.

The theoretical correctness of the monophyletic hypothesis may be conceded unconditionally without any necessity for admitting its practical correctness. Fundamentally the only correct view is that any definite phenomenon must have had a definite cause, and that

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* Many of Haeckel's works are known to English readers through excellent translations, as *The Nat. Hist. of Creation*, and the *Evolution of Man* (C. Kegan Paul & Co.).

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a repetition of the same causes in the realm of organic nature is simply impossible; thus the twofold origination of one and the same species from different parent forms brought into existence by dissimilar causes is physically inconceivable and hence impossible. Granted. The error and logically false conclusion involved in *Haeckelism* does not lie in this but in the presumption which asserts that the forms or individuals which it declares to belong to the same species must be identical. This they certainly are not, and though zoologists may include them under the concept of a 'species' this is done on extremely various grounds that are without exception of a subjective character. No one is competent to deliver an objective decision as to whether these or those individuals actually constitute only one, or two, or more species; the criteria for such a determination are wholly wanting. Moreover, the monophyletic hypothesis entirely ignores the fact that in by far the greater number of cases two individuals are needed for the propagation of new individuals, and these, irrespective of their sexual differences, certainly need not invariably belong to the same species; the possibility of hybridisation, *i.e.* the fertile union of two individuals of different species, is fully established. We know, moreover, that hybridisation is a favourite method employed by Nature for the origination of new forms—perhaps, indeed, the most powerful means at her command. Now, if the hybrid union of a species, A, with three others, B, C, D, results in each case in an analogous but different deviation from both parents, if this new character, common to the three families of hybrid progeny, A B, A C, and A D, justifies us, according to *our* subjective views, in establishing a new genus, we here have three different species of a second genus derived from the three originally different species, B, C, D; they have originated by a polyphyletic process. The Amphioxus is one of the cosmopolitan species, but the specimens from different localities exhibit some not inconsiderable differences. Now, if new forms were to arise from these dissimilar individuals, these might still possibly belong to one and the same genus; still, the Brazilian, the Philippine, the American, and the Australian species of this new genus would not have originated from a transformation of the descendants of a single pair, as the monophyletic hypothesis requires. I can make this discussion quite intelligible simply by quoting the following lines from Darwin: 'I will only remark,' he says, 'that if two species of two closely allied genera produced a number of new and divergent species, I can believe that these new forms might sometimes approach each other so closely that they would for convenience' sake be classed in the same genus, and thus two genera would converge into one.' Thus Darwin regards it as possible that the species of one and the same genus may have been derived from species not merely of one but of two different genera. All the most careful and recent investigations make it seem

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probable that the polyphyletic hypothesis is nearer to the truth than that which opposes it.

Note 115, *page* 301. These words had long been written when, quite lately, a paper came into my hands by Huxley on the affinities of fresh-water Crustaceans. According to him, the river Crustaceans of the northern hemisphere belong to one family, called by him *Potamobiidæ*, while those of the south he calls *Parastacidæ*. He points out that the two groups are easily distinguished by certain peculiarities in the structure of the gills, but he nevertheless suggests that the two forms, in themselves so distinct, might have descended from a common primitive form which peopled the tropical seas—where they are now for the most part wanting—and in their migrations into the rivers of the islands and continents of the north diverged into the structure of the *Potamobiidæ*, and in the south into that of the *Parastacidæ*.

Note 116, *page* 302. A notice of Tyndall's recent investigations may be found in *Nature* for 1877. The unprejudiced reader will here find, as it seems to me, an irrefutable disproof of 'Abiogenesis,' as it is called, and will be greatly interested in following the course of brilliant experiments, and the crowd of new facts elicited by them. Any further details are not here to the purpose, as Tyndall's experiments were made on the development of the germs of Fungi.

Note 117, *page* 312. In the centre of Mindanao, on the upper course of the Agusan, among the Manobos living there, I found a fossil elephant's tooth, which was worn by the Baganis, or chiefs, of that cannibal race on solemn occasions, such as going out to battle, strung on to a necklace with other objects, as small images of gods, crocodiles' teeth, &c. When a foe is killed, his breast is opened with the sacred sword, and all these objects, sacred to the god of war, are dipped in his blood; and it is not till the god has thus slaked his thirst in the blood of the enemy that the Bagani may eat a portion of the heart or lungs. Both the specimens of fossil elephant-teeth that I brought thence are now in the Ethnological Museum at Dresden.

CHAPTER XI.

Note 118, *page* 332. Compare Note 18 to Chap. III.

Note 119, *page* 335. It was formerly supposed that the slightly spiral tubes in the corals, in which the Sipunculidæ live, were the shells of a mollusc, and that the worms had first established themselves in them, and then the coral had formed upon them. This view was the result of a superficial examination; there can be no doubt that the worm settles on the coral, grows with it, and makes its own tube

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Note 120, *page* 352 The minute Copepod here described as living in the stomach of *Müllèria lecanora* is *Lecanurius intestinalis*.

Note 121, *page* 354. The following list is extracted from various papers in a German periodical, the *Zoological Garden*, edited by Dr. Noll, of Frankfurt. I have omitted such examples as have already been mentioned in the text.

Carnivora.

Polecat and ferret.
Wild cat and domestic cat.
African leopard and black panther of Java.

Ruminants.

Yak and common cow (at Halle).
Bison and black cattle.
Ovis musimon and *O. cycloceros*.
Cervus virginianus and *Cervus macrotis* (in Cincinnati).
Lina-sheep (in Chili), a cross between the sheep and goat—somewhat doubtful.
Cervus minor, a cross between the Axis and the Hog-deer.

Pachydermata
(with solid hoofs).

Equus tæniopus, M., and *Equus zebra*, Fem. (at Berlin).
Horse, M., and Burchell's zebra, F.
Ass, M., and Burchell's zebra, F.
Sus scrofa persica and *Sus scrofa sondaica* (at Rotterdam).

Rodents.

Lepus variabilis and *Lepus timidus*, in a free state.

Birds.

Modena pigeon, M., and turtle-dove, Fem.
Phasianus versicolor and Gold pheasant (at Antwerp).
Gold pheasant and *Thaumalia Amherstiæ* (at Paris).
Anas superciliosa and *Aix sponsa*.
Greenfinch and goldfinch.

Insects.

Phigalia pilosaria, M., and *Nysia hispidaria*, Fem. (as described by Midford). See Packard, *Guide to the Study of Insects*, p. 54.

CHAPTER XII.

Note 122, *page* 361. Similar relations exist between various other animals. The singular Nemertean *Malacobdella* lives almost everywhere, a solitary parasite in the branchial cavity of a mollusc; but we here have a very plausible explanation which is almost certainly the correct one, being confirmed by occasional observations of the co-exist-

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ence of two or three specimens in the same mollusc. When the young animal, having just found its way into its dwelling, begins to eat, it will catch at every organic object that is brought into the branchial cavity by the current, and so hinder a later comer from establishing itself in the same place. But an instance observed by K. Vogt is quite unintelligible without some such hypothesis as I have put forward in the text. Among hundreds of specimens of a species of Labrus, of which about 43 per cent. were attacked by a parasitic Crustacean, *Lepeophilus* only two were found which had two parasites, one on each side; all the others had but one, sometimes on the right and sometimes on the left; but the number of those that had settled on the right side was considerably greater than those on the left, as 27 to 16 per cent. They were always attached to the lateral line. What in this case can have hindered the establishment of several parasites on the same fish? As it seems to me, the only thing that proves unfavourable to a second parasite is some deterioration in the juices of the fish by the first.

Note 123, *page* 372. This assertion that no mollusca but these of the genus Onchidium have such dorsal eyes is based on the investigations, at once of great extent and of extreme anatomical accuracy, conducted by Bergh, of naked marine mollusca, and on my own researches, carried on with a view to this particular, into the structure of other land and water mollusca. Here and there, certainly, we find eye-like specks of pigment on the back or sides of the body, as in *Sphærodoris punctata* and *papillata* among the naked mollusca, and *Margarita* in the Conchifera, but all Bergh's researches and my own, with all the most modern instruments, show these to be merely concentrated spots of pigment with no connection in any instance with a nerve, and exhibiting no trace of the typical elements of a true eye.

Note 124, *page* 381. A case perfectly analogous to that of the Onchidium described in the text occurs among fishes of the family of Scopelidæ. These are deep-sea forms, to which indeed belong some of those described by Günther as having luminous organs; at the side of the body or on the belly they have a number—varying according to the species—of large silvery spots of different sizes, and which had already been spoken of as eyes by Leuckart in 1865. Still, until quite recently, the accuracy of this view had been doubted in spite of the statement of that very skilful naturalist. Quite lately, however, an exact description by Dr. Ussow (published in the *Bulletin* of Moscow) of the structure of certain eye-like spots in some bony fishes leaves no room for doubt, so far as I see, that Leuckart was perfectly right; all the attributes of true eyes are to be found in the genera *Chauliodus*, *Astronesthes*, and *Stomias*. But according to Ussow other species have organs in similar positions, which he designates as glands. I must confess that his representation has not convinced me of the accuracy of this interpretation, and I should venture to hazard an opinion on the

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contrary that these so-called glands are either illuminating organs, like those detected by Günther, or sensitive organs which have not yet been developed into eyes. The genera in which he has discovered these supposed 'pigmented glands' are *Scopelus*, *Gonostoma*, and *Maurolicus*. Finally, there are two genera, *Sternoptyx* and *Argyropelecus*, in which the pigment-cells existing in corresponding spots in the body are said to have a character between pigmented glands and true eyes.

Note 125, *page* 382. My brother, Georg Semper, has communicated to me the following case, lately observed by him, of the adaptation of an old species to the colour of new surroundings—or rather of its availing itself of it for protection. During the last ten years the well-known white-leaved variety of *Acer negundo* has been largely planted in gardens in Hamburg, and since this the common white cabbage butterfly has accustomed itself to settle by preference on this shrub. It is then extremely difficult, as my brother informs me, to distinguish the butterflies as they sit on the leaves, their yellowish colour being lost in that of the leaves. Here it is quite clear that the colour of the *Pieris* cannot have been produced by selection, since it had the same characteristic colouring long before the introduction of the white-leaved Maple. But if now one or another species or variety could benefit by the similarity of colouring which has thus accidentally arisen, in the struggle for existence, it would be at an advantage over any other species which was by any cause disqualified from availing itself of this protection, and thus the protective resemblance might occasion a selection among the different forms. In this case, beyond a question, selection had absolutely nothing to do with the origin of the protective colouring, and I am convinced that in many cases, if not in all, the occurrence of protective resemblance is not to be explained by selection. Some very interesting cases of protective mimicry are mentioned in *Brazil, the Amazons, and the Coast*, by Herbert Smith (Sampson Low & Co.), chap. vii.

Note 126, *page* 387. The pigment-forming matter—chromogene, as it is called—is conveyed by the blood to every organ in the body. It depends on local conditions whether it is in some places deposited in abundance and in others not at all. Consequently the primary distribution of colour depends on the structure of the organ or of that portion of the skin where such a deposit normally takes place. Examples to prove this are absolutely innumerable; they may be found in almost every animal. The gay colours of many shells—both bivalve and univalve—are in great measure produced by the deposition of pigment in the external organic skin, which covers the calcareous portion of the shell; the pigment itself is elaborated by glands which exist exclusively in the margin of the mantle. It is according to the regularity of the arrangement of these pigment-glands and the interruption in the exercise of their functions that certain patterns and colours occur in the shells—

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spots, stripes, bands, or zig-zag lines, &c. In butterflies the microscopic scales on both surfaces of the wings have the pigment deposited in them; in quadrupeds it is in the hair, in birds in the feathers; here the distribution of colours must depend on the affinity of these organs for the chromogenes, and, consequently, indirectly on those organs which grow out of the skin. But the usefulness of certain colouring, which does not occur until later, can have no influence on the origination of these organs or on the different degrees of affinity of these parts to the chromogenes; hence it follows that it is only by the more or less regular arrangement of such organs that animals can acquire a mode of colouring which corresponds with similar regular colouring in the surrounding objects. Hence a striped butterfly can never originate directly from an irregularly spotted one by natural selection, since this presupposes a previous transformation in the organs containing the colours; but if, through any physiological cause acting in the organism, the spotted colouring had already been altered to any considerable extent to a striped arrangement, then selection might gradually lead to the extermination of the spotted variety by augmenting any protective resemblances the striped form might possess. But it would, of course, be absurd, in such a case as this, to speak of selection as the primary cause of the mode of colouring.

Note 127, *page* 389. *Sesia apiformis, vespiformis, crabroniformis*, &c.

Note 128, *page* 397. According to Quug a Gaimaro, the species of *Harpa*, a marine univalve, possess the same peculiarity as *Polydontes*, *Stenopus*, and *Helicarion*. Although I have caught a considerable number of living specimens, I never discovered this by my own experience. At any rate, the mode in which Harpa sheds its foot is quite different from that of the species of Helicarion. If by some extraordinary accident it is unable to withdraw its foot, which is very large, into its shell, it presses it against the sharp edge of the shell, and so cuts off the hinder portion of it in order to protect itself.

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